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ANATOMICAL ASPECTS OF *DRESSLERELLA* (ORCHIDACEAE)

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Dresslerella Luer, a recently described genus in the subtribe Pleurothallidinae, consists of eight species ranging from Nicaragua to Peru. According to Luer (1976), the genus is characterized by dark-green leaves suffused with purple; minutely ciliate leaf margins and entire leaf apices; fleshly, saccate flowers with concave, adnate lateral sepals; and four pollinia, a feature which immediately distinguishes it from *Cryptophoranthus* Barb. Rodr. and *Pleurothallis* R. Br. which have only two pollinia. The most recent additions to *Dresslerella* include two new species and two transfers from *Restrepiella* Garay & Dunsterville treated by Luer (1978a).

This report initiates a series of anatomical studies of genera within the Pleurothallidinae, a subtribe of well over 3,000 species in the neotropics. Important literature particularly relevant to this undertaking are studies by Hunecke (1904), Haberlandt (1914), Solereder and Meyer (1930), Cheadle (1942), Stebbins and Khush (1961), Rosso (1966), Ayensu and Williams (1972), Tomlinson (1974), Williams (1974, 1976, 1979), and Withner, Nelson, and Wejksnora (1974). In subsequent installments cytological and palynological aspects of this vast and often bewildering tribe will be examined in the hope that these taxonomic characters, taken with floral characters, will help us understand intra- and intergeneric relationships.

MATERIALS AND METHODS

Living plants of all species examined are now housed at Florida State University and voucher specimens are deposited at the Marie Selby Botanical Gardens (SEL). Material of *Dresslerella hirsutissima* (C. Schweinf.) Luer and *D. pilosissima* (Schltr.) Luer and roots of *D. caesariata* Luer were unavailable for study.

Epidermal scrapes of leaves were made from either fresh or preserved material with a razor blade, mounted in glycerine:ethanol (3:1), observed with a Wild M 20 microscope under bright field, and photographed with a Nikon M-35 camera.

Freehand transverse sections of leaves, secondary stems, and roots were mounted on glass slides in Toluidine Blue 0, and observed and photographed as above. Leaf sections were made approximately halfway between the base and apex. Tissue macerations were performed according to Jeffrey's method as outlined in Johansen (1940). Microtome-sectioned materials were first fixed in formalin-propionic acid-alcohol (FPA) for at least 24 hours, dehydrated in a tertiary-butyl alcohol series, and embedded in Paraplast. Sections were then stained with safranin, fast-green, and orange-G prior to photographing them.

For scanning electron microscopy freehand sections were fixed in FPA, dehydrated through an acetone-water series, and then critical point dried with CO_2. Specimens were next mounted on aluminum stubs covered with Scotch brand double-stick tape, coated in vacuo with gold-palladium, and examined in a Cambridge Stereoscan S4-10 scanning electron microscope at an accelerating voltage of 10 kv. Observations were recorded on Polaroid film and the negatives contact printed later.

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OBSERVATIONS

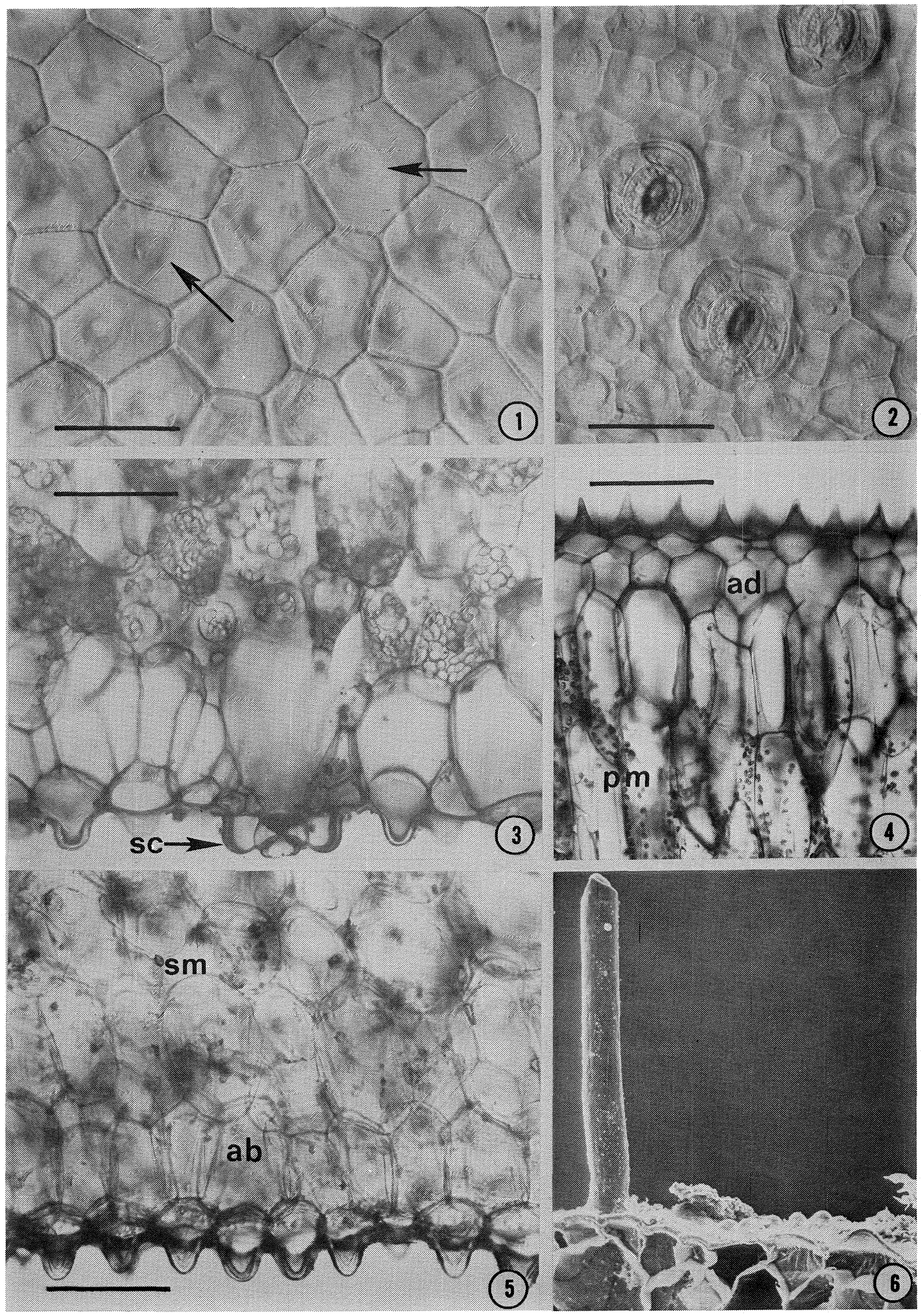
Leaf Anatomy

EPIDERMIS. In surface view almost every cell on both the adaxial and abaxial epidermal surfaces possesses a central papilla (Figs. 1, 2). However, the cells immediately surrounding stomata and glandular trichomes, which will be discussed shortly, lack these papillae (Figs. 3 and 29, respectively). The apices of the papillae are generally acute to acuminate (Fig. 4), although the papillae on the abaxial epidermis of *Dresslerella hispida* (L. O. Williams) Luer, *D. powellii* (Ames) Luer, and *D. caesariata* Luer are characteristically blunt and obtuse (Figs. 3, 5). Unicellular trichomes, much longer than the papillae, occur on the leaf margins in groups of three or four for all species. Leaves of *D. caesariata* are unique in having this second type scattered over the adaxial and abaxial surfaces as well as along the margins (Figs. 6, 14). Such distributions agree with Luer's findings (1978a). Parenthetically, we note that the sepals of *Dresslerella stellaris* Luer & Escobar are invested with highly unusual stellate trichomes which branch horizontally (Figs. 7, 8; see Luer, 1978a).

Adaxial and abaxial epidermal cells range in shape from rectangular to polygonal in surface view (Figs. 1, 2, 30) and are overlaid with a rather thin, smooth cuticle. Adaxial cells are slightly larger than the abaxial cells in all species examined. In transverse section, the epidermal cells vary in shape. *Dresslerella powellii* and *D. stellaris* possess diamond-shaped cells while the other species have triangular to peg-shaped types. Elliptical to rectangular shapes are also frequent for all species. Cell walls with conspicuous pit canals (Figs. 1, 2, 30) are uniformly thin except for *D. caesariata* where there are slight thickenings on the outer tangential walls. Anthocyanin-like compounds are often present in the epidermal cells of all species, and especially in the subsidiary cells of *D. pertusa* (Dressler) Luer.

Stomata are restricted to and raised above the abaxial epidermis. The subsidiary cells, also elevated, number from four to six (seven occurring rarely in *D. pertusa* and *D. hispida*) and are arranged as a wreath around the guard cell pair (Figs. 2, 9, 10, 30). In transverse section the axis of the subsidiary cells is vertical for all species with the exception of *D. pertusa* in which the cells gently slope so that they are no lower than the cuticular ridges of the guard cells. Average heights of the subsidiary cells are shown in Table 1. Stomata with 5, 6, or 7 subsidiary cells are probably formed by one or two transverse divisions of the two lateral cells from a four-cell configuration, but ontogenetic studies are needed to establish the precise pattern of subsidiary cell development. Mean lengths and widths of the guard cell pairs for the six species are listed in Table 1. Conspicuous substomatal chambers also occur in all species (Figs. 3, 11).

Glandular trichomes are present and sunken in both leaf surfaces of all species. These change radically in morphology during leaf development. The trichome apparatus of young leaves consists of (1) a globose, thin-walled apical cell with a nucleus several times larger than those of epidermal cells, and (2) a clavate stalk cell with heavily cutinized lateral walls embedded in hypodermal tissue (unpublished results). At this stage in leaf ontogeny guard cell meristemoids have not divided and differentiated into guard cells. Just prior to guard cell differentiation, the apical cells of these trichomes fill with a brown mucilage and rupture (Haberlandt, 1914; Uphof, 1962).



Figures 1-6. Fig. 1. *Dresslerella pertusa*. Adaxial surface of leaf showing one central papilla in each epidermal cell (at arrows) and conspicuous pit canals. Light microscope (LM) photograph. Scale bar equals 50 μm Fig. 2. *Dresslerella hispida*. Abaxial epidermal surface of leaf with three stomata. The central stoma has four subsidiary cells and the lower stoma has five subsidiary cells. LM photograph. Scale bar equals 50 μm Fig. 3. *Dresslerella powellii*. Transverse section of leaf showing abaxial epidermis, papillae, stomatal guard cells, and subsidiary cells (sc). LM photograph. Scale bar equals 50 μm. Fig. 4. *Dresslerella elvallensis*. Transverse section of leaf. Adaxial epidermis with acuminate papillae, adaxial hypodermis (ad) and palisade mesophyll (pm). LM photograph. Scale bar equals 100 μm Fig. 5. *Dresslerella powelli*. Transverse section of leaf. Abaxial epidermis with obtuse papillae, abaxial hypodermis (ab) and spongy mesophyll (sm). LM photograph. Scale bar equals 50 μm. Fig. 6. *Dresslerella caesariata*. Transverse section of leaf. Adaxial epidermis showing trichome and papillae. Scanning electron microscope (SEM) photograph. × 200.

A brown opaque residue then fills the epidermal depression (Fig. 29). Later in leaf development, two or more pitted cells develop at the base or foot of the stalk cell (Figs. 12, 29). Solereder and Meyer (1930) reported the presence of sunken hairs throughout the Orchidaceae based upon the investigations of Mobius (1887) and several others.

HYPODERMIS. From our ontogenetic studies, hypodermal cells are derived from divisions of ground tissue rather than from periclinal divisions of protodermal cells which would result in a multiple epidermis (Esau, 1960). A true adaxial hypodermis is present for all species and shows some variation in extent. All but one species possess a hypodermis consisting of 1-2 layers of thin-walled, large cells (Fig. 13). The adaxial hypodermis of *D. caesariata* is exceptional in having 4-5 layers. These cells, only rarely containing chloroplasts, range in shape from transversely elongate polygonal, rectangular, elliptical, to irregular. *Dresslerella stellaris* and *D. powellii* exhibit some trapezoid and barrel-shaped cells as well. A uniseriate abaxial hypodermis formed by thin-walled, rectangular to polygonal cells is constant for all six species. Spiral wall thickenings, present in the leaves of several other pleurothallid genera (unpublished results), are entirely absent from hypodermal cells in all *Dresslerella* species.

MESOPHYLL. The mesophyll is consistently bifacial. The palisade tissue consists of from 2-6 layers of rectangular, elliptical, trapezoidal, and/or polygonal cells. *Dresslerella caesariata* possesses the fewest palisade layers (2-3) and *D. hispida* the most (6). Spongy mesophyll with small intercellular spaces is confined to the lower third of the leaf (Fig. 14). Cells are usually isodiametric to elliptical, although polygonal shapes also occur. Several pitted regions on the walls of most spongy mesophyll cells are very prominent in all species (Figs. 14, 15). These regions correspond to the "cone-parenchyma" described in Solereder and Meyer (1930) for several epiphytic orchids.

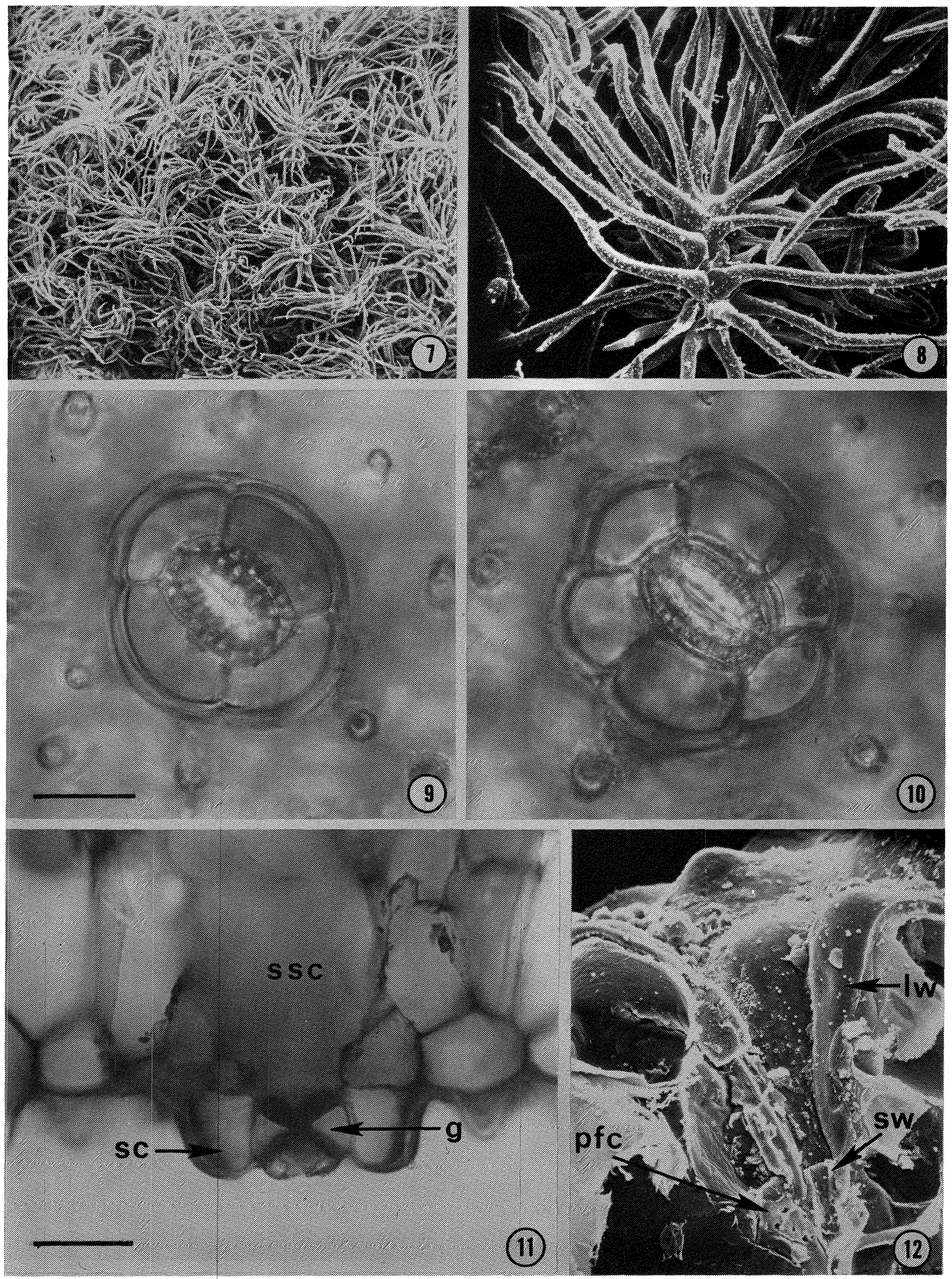
VASCULAR BUNDLES: As viewed in transverse section, collateral vascular bundles are arranged in a single row at the juncture of palisade and spongy mesophyll, except in *D. pertusa* which has two rows. Variation in number of vascular bundles present in the middle of the leaves of the six species is shown in the table. The disparity between the numbers of *D. hispida* and *D. powellii* and the numbers of the others can be partially explained by the simple fact that the former species possess the smallest leaves of the genus.

Veins are of three sizes in all taxa and their size ratios are presented in the table. Type I bundles, the largest and fewest in number, typically possess a well-developed abaxial sclerenchyma cap (Fig. 16) and fewer fibers at the adaxial pole. The abaxial sclerenchyma caps of Types II and III are similarly extensive but few, if any, fibers are present adaxially. Commissural veins occur in all species.

Xylem is composed of tracheids with annular, helical, or scalariform thickenings and xylem parenchyma (Fig. 16). Vessels are absent. Phloem consists of sieve-tube elements, companion cells, and phloem parenchyma. With the exception of *D. elvallensis* Luer, a sclerenchymatous bridge separates the xylem and phloem tissues. Discrete fiber bundles, characteristic of the Oncidiinae (Ayensu and Williams, 1972; Williams, 1974) and other orchidaceous groups, are lacking in *Dresslerella*.

TABLE 1

SPECIES CHARACTER	*D. caesariata*	*D. elvallensis*	*D. hispida*	*D. pertusa*	*D. powellii*	*D. stellaris*
Mean height of subsidiary cells	28 μm	16.8 μm	25.2 μm	9.8 μm	28 μm	14 μm
Mean lengths and widths of guard cell pairs	52.6 x 40 μm	50.4 x 33 μm	38.9 x 36.4 μm	52.9 x 40.6 μm	49.6 x 38.4 μm	54.6 x 35.3 μm
Number of vascular bundles at middle of leaf	17	17-19	13	39	13	18-19
Vascular bundle size ratio Type I : Type II : Type III	1 : 1.3 : 2	1 : 1.6 : 2	1 : 1.6 : 2	1 : 1.3 : 1.8	1 : 1.3 : 1.7	1 : 1.2 . 1.6
Number of vascular bundles at middle of secondary stem	18	30	28	34	21	20



Figures 7-12. Figs. 7 and 8. *Dresslerella stellaris*. Epidermal surface of sepal showing branched, stellate trichomes. SEM photographs. Fig. 7, X 21.5. Fig. 8, X 105. Figs. 9 and 10. *Dresslerella elvallensis*. Abaxial epidermis of leaf with stomata surrounded by wreath-like configurations of subsidiary cells. Fig. 9, four subsidiary cells. Fig. 10, six subsidiary cells. LM photographs. Scale bar equals 20 μm Fig. 11. *Dresslerella powellii*. Transverse section of leaf. Stomatal apparatus with four subsidiary cells (sc), two guard cells (g), and a large substomatal chamber (ssc) visible. LM photograph. Scale bar equals 20 μm. Fig. 12. *Dresslerella caesariata*. Transverse section of leaf. Abaxial glandular trichome apparatus with thickened lateral walls (lw), stalk cell wall (sw), and two pitted foot cells (pfc). SEM photograph. X 800.

Secondary Stem Anatomy

As Rosso (1966) has noted, the leaf anatomy of orchids has been treated thoroughly, often at the expense of stem and root investigations, in part because the leaves are easier to procure. We might add that stem and root characters seem to show less variation than leaves at the specific and often generic levels and so perhaps have been regarded as less useful taxonomically. Nevertheless, to reach fully objective conclusions, as many characters as possible should be considered. As used here, the term "secondary stem" refers to the vertical axis supporting the leaf, and "primary stem" refers to the rhizome.

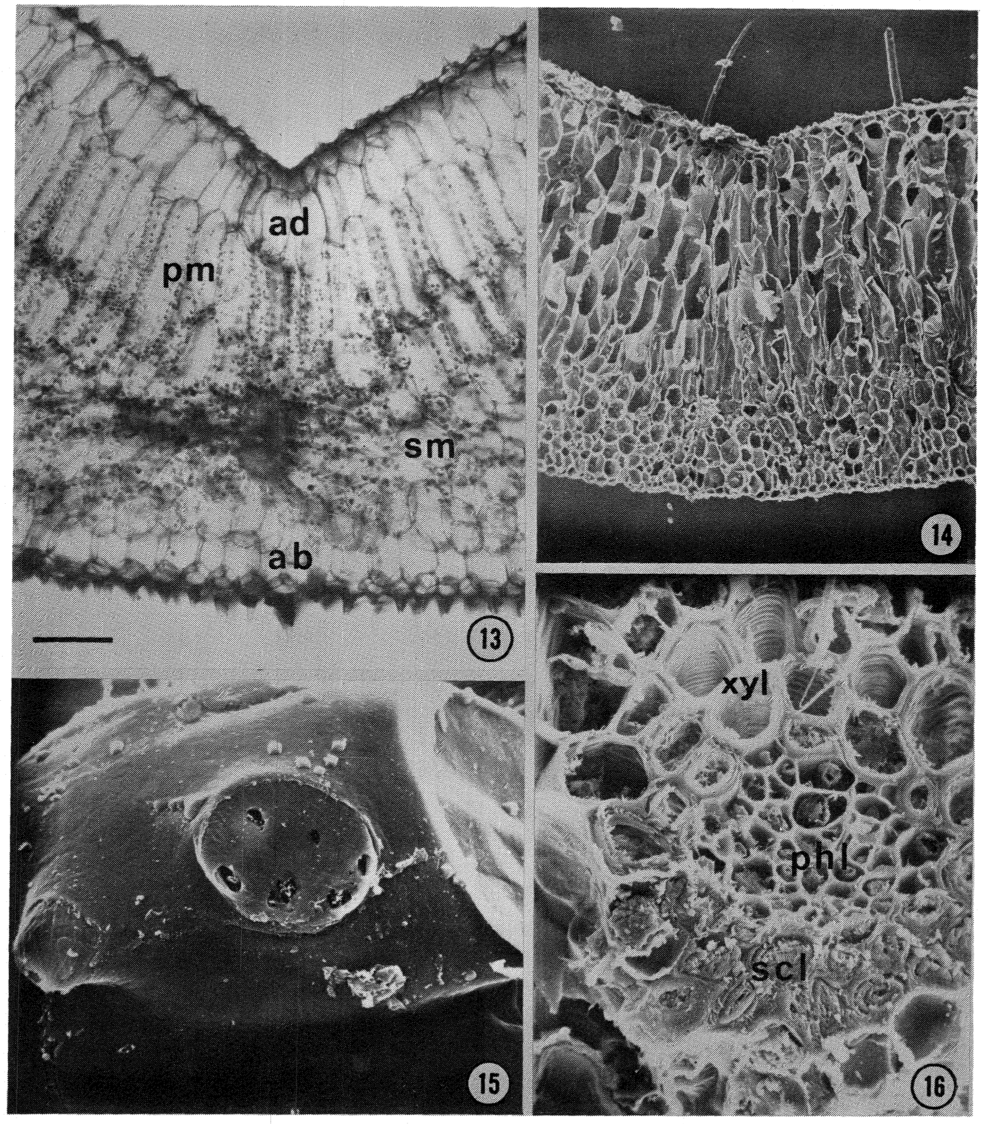
EPIDERMIS. A rather thick cuticle extends over the epidermal surfaces of all species except *D. hispida*. Substantial differences in trichome size and shape exist among the six species. The epidermal cells of *D. elvallensis* (Fig. 17) possess relatively long papillae with acuminate tips. On the other hand, *D. pertusa*, *D. hispida*, and *D. stellaris* lack developed papillae (Fig. 18). The development of papillae in *D. powellii* and *D. caesariata* is intermediate between these two extremes. Epidermal cell shape varies between elliptical, peg-shaped, and polygonal types. Stomates do not occur on the stem in any species. Epidermal cells only rarely contain chloroplasts.

CORTEX. The extent of the cortex is very irregular in each species because the vascular cylinder is consistently eccentric. Accordingly, *D. elvallensis* and *D. hispida* have a cortex ranging from 4 to many layers. In the other species the cortex consists of 3-7 layers. Cells are isodiametric, elliptical, ovate, or occasionally polygonal in outline and thin-walled (Figs. 17, 18). Numerous chloroplasts occupy cortical cells.

VASCULAR CYLINDER. A phloic fiber sheath delimits the cortex proper from the pith in all species (Figs. 17, 18). *Dresslerella caesariata* and *D. pertusa* are exceptional in possessing an intermittent, subepidermal sclerenchymatous ring also. Fewer fibers are disposed along the xylem pole of vascular bundles. An inner ring of fewer bundles is either embedded in the ground parenchyma (Fig. 18) or else continuous with the phloem fibers of the outer ring (Fig. 17). This two-concentric-ring configuration is comparable to that reported for *Physosiphon loddegesii* Lindley and *Restrepia guttulata* Lindley by Solereder and Meyer (1930). The number of vascular bundles at the middle of the secondary stem for each of the species is listed in the table.

Individual bundles for all species are collateral, xylem internal with centrifugal maturation and phloem external (Fig. 19). As in the leaves, a uniseriate sclerenchymatous bridge separates xylem and phloem in some but not all vascular bundles in each species. Xylem tissue consists of xylem parenchyma, xylem fibers, and tracheids with annular, helical (Fig. 20), or scalariform (Fig. 21) secondary thickenings. Occasionally metaxylem tracheids with oval bordered pits are also present (Fig. 22). Again, vessels are absent. Phloem consists of sieve-tube elements, companion cells, and phloem parenchyma. Silica-bodies are associated with some vascular bundles.

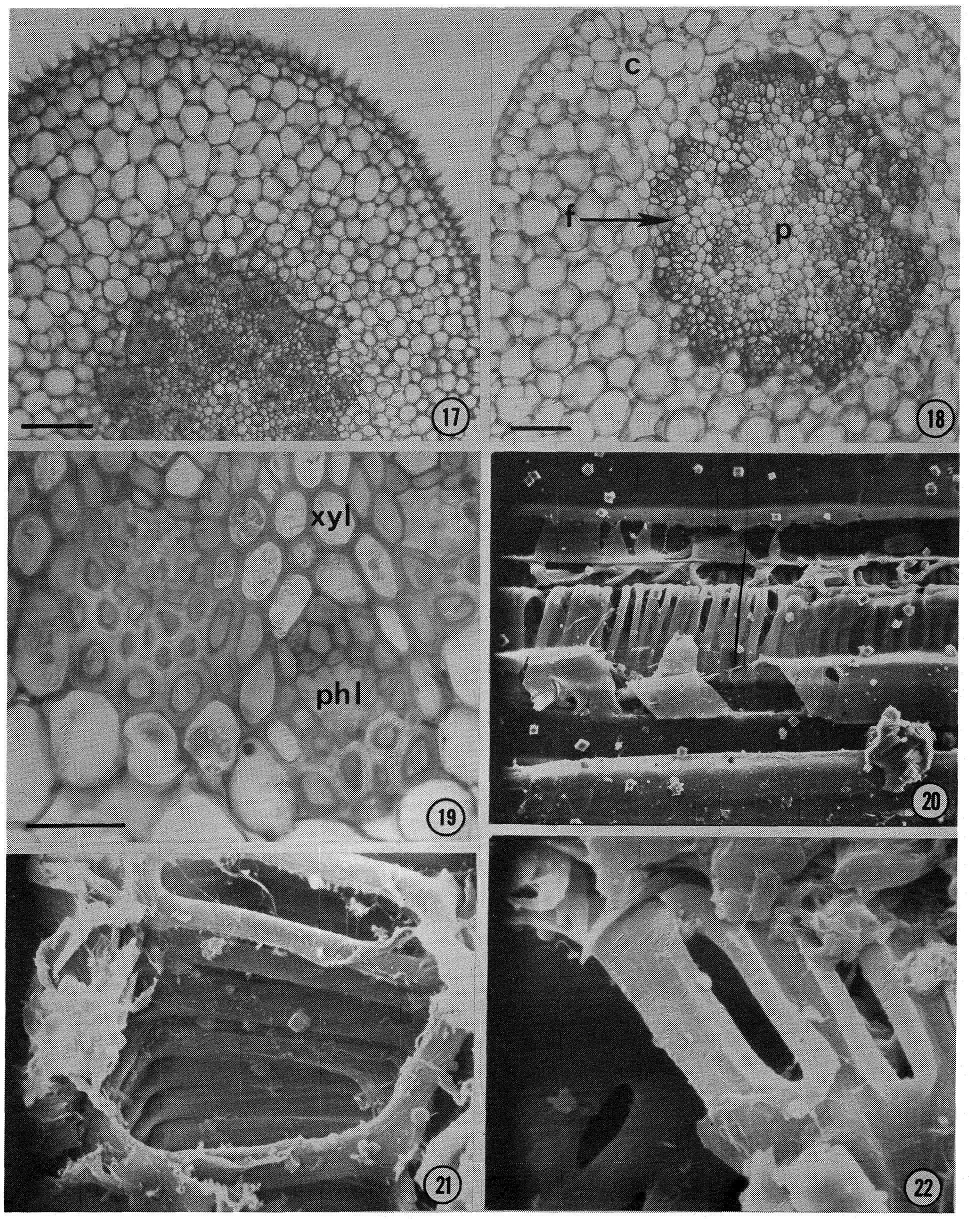
PITH. A parenchymatous pith of thin-walled cells is a constant feature of all species. Usually, however, its extent is limited to relatively few cell layers in diameter (Figs. 17, 18). Cells are typically isodiametric, ovate, or elliptical in shape.



Figures 13-16. Fig. 13. *Dresslerella pertusa.* Transverse section of leaf through midrib. Note adaxial hypodermis (ad), abaxial hypodermis (ab), palisade mesophyll (pm), and spongy meosphyll (sm). LM photograph. Scale bar equals 100 μm Fig. 14. *Dresslerella caesariata.* Transverse section of leaf through midrib. Note palisade and spongy mesophyll. SEM photograph. × 37. Fig. 15. *Dresslerella caesariata.* Spongy mesophyll cell of leaf. Note pitted region. SEM photograph. × 2100. Fig. 16. *Dresslerella caesariata.* Transverse section of leaf. Vascular bundle showing abaxial sclerenchyma cap (scl), phloem (phl), and xylem tracheids (xyl). SEM photograph. × 1000.

Root Anatomy

EPIDERMIS. The root epidermis of all species studied consists of a two-layered velamen. Cells are either elliptical, rectangular, or polygonal in transverse section (Figs. 23-25). In all species but *D. powellii*, both tangential walls are thickened with thickenings continued onto radial walls (Fig. 23). This agrees with observations for other species in the Pleurothallidinae



Figures 17-22. Fig. 17. *Dresslerella elvallensis.* Transverse section of secondary stem. Note acuminate epidermal papillae. LM photograph. Scale bar equals 100 µm. Fig. 18. *Dresslerella hispida.* Transverse section of secondary stem showing absence of epidermal papillae, cortex (c), phloic fiber sheath (f), two concentric rings of vascular bundles, and pith (p). LM photograph. Scale bar equals 50 µm. Fig. 19. *Dresslerella elvallensis.* Transverse section of secondary stem. Three vascular bundles with abaxial sclerenchyma cap, phloem (phl), and xylem (xyl). LM photograph. Scale bar equals 20 µm. Fig. 20. *Dresslerella hispida.* Longitudinal section of secondary stem. Shown here is a xylem tracheid with helical thickenings. SEM photograph. X 1050. Fig. 21. *Dresslerella caesariata.* Longitudinal section of secondary stem. Xylem tracheid with scalariform thickenings. SEM photograph. X 5000. Fig. 22. *Dresslerella hispida.* Longitudinal section of secondary stem. Metaxylem tracheid with oval bordered pits. SEM photograph. X 10,000.

(Solereder and Meyer, 1930). In *D. powellii* all walls are either uniformly thickened or slightly thicker on the inner tangential walls (Figs. 24, 25). Unicellular root hairs with active protoplasts are present in all species (Fig. 23). Rodlike bodies reported by Meinecke (Solereder and Meyer, 1930) for many pleurothallid genera are absent.

EXODERMIS. A uniseriate exodermis is situated between the velamen and cortex proper. In transverse section its cells are square to polygonal and thickened on all walls or only on the outer tangential and radial walls (Figs. 23 - 26). Following the terminology set forth by Solereder and Meyer (1930) and continued by Rosso (1966), these two types of exodermal cells are designated 'O' -cells and 'U' -cells, respectively. The exodermis of *D. stellaris* is consistently an 'O' type (Fig. 23), *D. elvallensis* and *D. pertusa* are consistently 'U' type (Fig. 26), and *D. hispida* and *D. powellii* have 'O' and 'U' types (Figs. 24, 25). In longitudinal section the exodermis of all species consists of files of alternating long rectangular cells and short square cells called passage cells by Solereder and Meyer (1930) and Rosso (1966). Passage cells retain their protoplasts at maturity while the long cells usually do not.

CORTEX. Exclusive of the exo- and endodermis, the cortical parenchyma of all species does not extend beyond seven layers. The cells immediately adjacent to both exo- and endodermis are characteristically smaller than the cells of the central layers. Cell shape ranges from isodiametric to elliptical and polygonal (Figs. 23 - 27). Raphides are common in cortical cells of all species.

ENDODERMIS. All species possess a uniseriate endodermis consisting of thickened, "protective" (Solereder and Meyer, 1930) cells and thin-walled passage cells. Thickened cells are again either 'O' -cells or 'U' -cells. *Dresslerella pertusa* possesses a 'U' type endodermis (Figs. 26, 27) and the other species an 'O' type endodermis (Figs. 23, 25, 28). Passage cells are opposite the protoxylem points. Cells are rectangular, elliptical, triangular, or polygonal in transverse section.

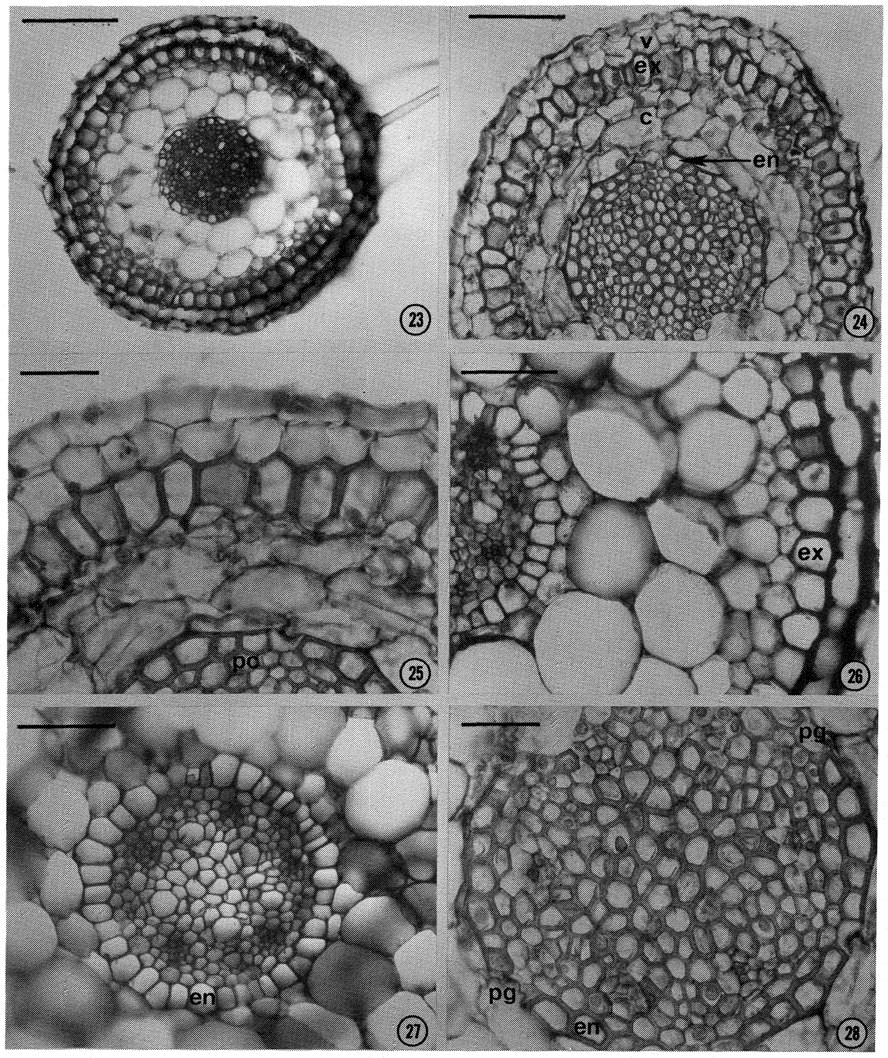
VASCULAR CYLINDER. In *Dresslerella* the vascular cylinder or stele consists of the outermost pericycle, xylem, and phloem. All species lack a parenchymatous pith. The core of the root is occupied instead by metaxylem vessels and fibers.

All species possess a uniseriate pericycle of isodiametric, rectangular, elliptical, and/or polygonal cells. Thin-walled parenchyma cells occur opposite the protoxylem elements and lignified cells abut on protophloem cells (Figs. 23, 24, 27, 28).

The steles of all species are polyarch, the xylem and phloem alternating with each other in radial fashion. The root of *D. hispida* has 4 protoxylem points (and 4 corresponding phloem areas) and *D. pertusa* possesses 5 (Fig. 27). Other species are hexarch (Figs. 23, 28). Xylem consists of tracheids with annular, helical, or scalariform thickenings, vessel elements with scalariform thickenings or pitted walls and with simple perforations, xylem parenchyma, and xylem fibers. Phloem comprises sieve-tube elements, companion cells, phloem parenchyma, and phloem fibers.

DISCUSSION

From these observations a very distinctive combination of anatomical characteristics is evident for the genus *Dresslerella*. Long, uniseriate tri-



Figures 23-28. Figs. 23 and 24. *Dresslerella stellaris*. Transverse sections of root. Note two-layered velamen (v), unicellular root hair, 'O' type exodermis (ex), cortex (c) and 'O' type endodermis (en). LM photographs. Scale bar in Fig. 23 equals 100 μm. Scale bar in Fig. 24 equals 50 μm. Fig. 25. *Dresslerella powellii*. Transverse section of root showing velamen, exodermis, cortex, endodermis, and uniseriate pericycle (pc). LM photograph. Scale bar equals 20 μm. Figs. 26 and 27. *Dresslerella pertusa*. Transverse sections of root. A 'U' type exodermis (ex), 'U' type endodermis (en), and a pentarch stele are visible. LM photographs. Scale bars equal 50 μm. Fig. 28. *Dresslerella powellii*. Transverse section of root with 'O' type endodermis (en) and passage cells (pg) opposite protoxylem points. The stele is hexarch. LM photograph. Scale bar equals 20 μm.

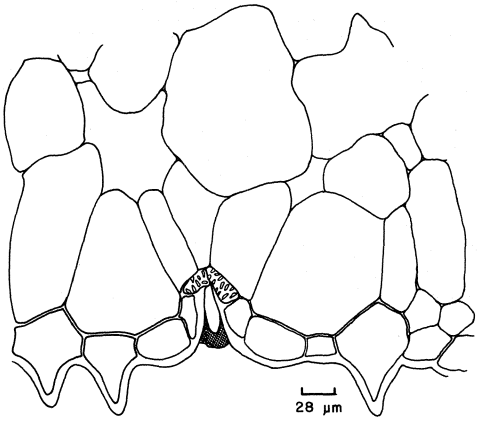


Figure 29. *Dresslerella elvallensis.* Camera lucida drawing of transverse section of mature leaf showing abaxial epidermis and papillae. A sunken glandular trichome with stalk cell and two pitted cells at the base is depicted. Hatched region represents a mucilage deposit.

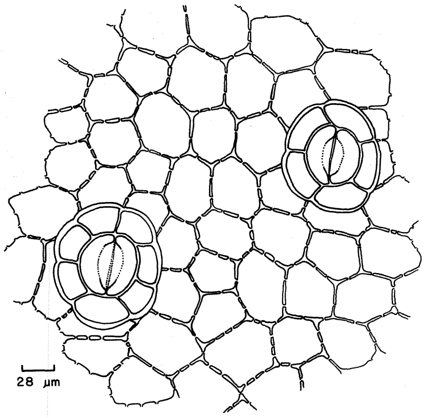


Figure 30. *Dresslerella hispida.* Camera lucida drawing of abaxial epidermis of leaf. Two stomata, one with five subsidiary cells and one with seven subsidiary cells, are represented. Note conspicuous pit canals. Papillae have not been included for the sake of clarity.

chomes and papillose trichomes over the leaf epidermis of all examined species are two such characteristics. Solereder and Meyer (1930) and Rosso (1966) report glandular and non-glandular trichomes for the Cypripedioideae. Solereder and Meyer (1930) also depict the leaf epidermal papillae of *Goodyera discolor* Ker., which closely resemble those in *Dresslerella* species. Long trichomes and papillae, taken by themselves, seem to be rare in the Orchidaceae; the combination of both is extremely rare in the Orchidaceae as a whole, and particularly within the Pleurothallidinae (unpublished results). Papillose stem epidermal cells of some *Dresslerella* species are equally valuable taxonomically since they occur in no other genera examined to date.

The wreath-shaped stomatal apparatus with 4-7 elevated subsidiary cells, common to all *Dresslerella* species, has been observed in only three other species -- *Pleurothallis pan* Luer, *P. alexandrae* Schltr., and *P. pastacensis* Luer -- from over 90 species in 14 pleurothallid genera examined to date. These three *Pleurothallis* species and a few more related ones seem to form another natural genus based upon a number of other vegetative and floral characters and will eventually be segregated (Luer, pers. comm.).

Other leaf features which combine to establish *Dresslerella* as a natural genus are an adaxial hypodermis of 1-2 (or rarely 4-5) layers, a uniseriate abaxial hypodermis, absence of spiral thickenings in the hypodermal and mesophyll cells, bifacial mesophyll, cone-parenchyma and crystalline inclusions in the spongy mesophyll.

The eccentric vascular cylinder of the secondary stem has been observed only in *Dresslerella*, and that this should occur in all of its species is at least interesting if not definitive in its own right. Also common to the secondary stem of all species is a phloic fiber sheath and a two-concentric-ring arrangement of vascular bundles.

Roots of *Dresslerella* are characterized by a two-layered velamen, uniseriate exo- and endodermis with passage cells, uniseriate pericycle, and absence of a parenchymatous pith.

Dresslerella pertusa may be separated from the other species by a number of unique characteristics, including relatively short subsidiary cells sloped in transection, highly disparate numbers of leaf and stem vascular bundles (39 and 34, respectively), a 'U' type endodermis, and 5 protoxylem points. *Dresslerella hispida* and *D. powellii* appear *prima facie* to be closely related, but anatomical analyses cannot confirm this. Although they both possess 13 leaf vascular bundles, obtuse leaf papillae, both 'O' and 'U' type exodermis, and an 'O' endodermis, nevertheless they differ in several other characters, such as the number of protoxylem points, presence of stem papillae, and leaf epidermal cell shape.

The genus possesses several structural features which, from preliminary investigations, are consistent for other genera and species in the Pleurothallidinae. Most pleurothallid leaves possess a hypodermis ad- and abaxially [the newly segregated genus *Dracula* Luer (1978b) is a notable exception]; bifacial mesophyll (again *Dracula* is an exception) with palisade mesophyll varying in degree of development; veins of 2-3 sizes; mesophyllous cone-parenchyma; and no discrete fiber bundles. All pleurothallid secondary stems observed to date possess a phloic sclerenchyma sheath and some may in addition exhibit a subepidermal or pericyclic fiber layer(s). Roots show little variability in possessing a multiseriate velamen, a uniseriate exo- and endodermis with passage cells, a uniseriate pericycle, and metaxylem elements forming the core in lieu of a parenchymatous pith. Cheadle (1942) has reported the same generality for the Orchidaceae and Rosso (1966) for the Cypripedioideae.

Few pleurothallids studied lack glandular trichomes, the morphology of which can vary slightly between species in terms of size and shape of apical cell, configuration of associated cells, and depth within surface tissues. Solereder and Meyer (1930) have depicted a variety of trichome-hydathodes in orchid leaves. These "active" glandular hydathodes should be distinguished from "passive" hydathodes composed of thin-walled cells situated between the epidermis and tracheid bundles and which secrete water by simple filtration (Haberlandt, 1914; Esau, 1960). Active hydathodes, or "water glands" (Esau, 1960), characterize many tropical epiphyte families, especially the Piperaceae (Solereder and Meyer, 1930), Araceae, Gesneriaceae, as well as Orchidaceae. Passive hydathodes have been observed in Umbelliferae and Compositae (Haberlandt, 1914), Ranunculaceae (Stevens, 1956), Acanthaceae (Reams, 1953), and many other families (Stocking, 1956). Reams (1953) has studied the ontogeny of active hydathodes in the aerial leaves of *Hygrophila polysperma* T. Anders (Acanthaceae).

Whether or not the glandular trichomes in the Pleurothallidinae should in fact be called "active hydathodes" or even "water glands" has not been confirmed. Tests for the presence of oil with Sudan IV proved negative. We have not observed guttation, nor have we had success with attempting to induce it in mature leaves. However, water secretion may be restricted to a certain stage in ontogeny of the trichome (Uphof, 1962), in this case only when the apical cell is intact in very young leaves.

Preliminary experiments with eosin stain on the water-absorbing capacity of mature leaves indicate that water is able to penetrate the epidermis to some extent, presumably between the lateral walls of a trichome depression and the cutinized walls of the stalk cell. Pitted cells, which only occur in mature leaves, would facilitate water movement into the water-storing hypodermal cells. Pitted cells also occur at the foot of absorbing scales of *Tillandsia* (Tomlinson, 1969) and of pearl glands of some *Peperomia* species (unpublished results).

Further research in this area is now in progress on the apical cells of glandular trichomes which mature and rupture in synchrony with guard cell differentiation. Apical cells possibly function in water secretion only when transpiration is suppressed or impossible during leaf ontogeny.

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