TRICHOMES AND STOMATA OF *GORDONIA LASIANTHUS* (THEACEAE)

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ABSTRACT

Study of trichomes and stomata on epidermal surfaces using the scanning electron microscope is presented with augmentation from sectioned and imprinted materials viewed using the light microscope. Trichomes always occur on flowers and abaxial leaf surfaces; they rarely occur on epidermis of mature twigs. The trichomes are mostly in fascicles of two to four parallel hairs; they vary in density and size. Stomata are cyclocytic with prominent stomatal rims and peristomatal rims, the latter usually in the form of buttressed cups. Comparisons are made with trichomes and stomata of related taxa.

The loblolly bay, *Gordonia lasianthus* (L.) Ellis, ranges from medium-sized shrubs to handsome trees up to 84 feet tall. It has leathery evergreen leaves and occurs in bay forests, low woods, and ti-ti swamp margins on the coastal plain from North Carolina to Florida, west to Mississippi. All other species of *Gordonia* (ca 30) occur in Asia.

Most writers (Bailey, 1949; Kurz and Godfrey, 1962; Radford et al., 1964; Small, 1933; and Wood, 1959) describe the leaves of *G. lasianthus* as glabrous; however, Metcalfe and Chalk (1950) recorded foliar hairs in fascicles with unicellular rays for *Gordonia* and *Ternstroemiopsis* (= *Eurya*) without reference to any particular species. Keng (1962), in his extensive treatment of the Theaceae, noted Melcalfe and Chalk's statement but wrote: "I observed such trichomes only in *Franklinia al{a}tamaha* and *Laplacea grandis*. They are not found in *Gordonia axillaris, G. gigantiflora, G. lasianthus*, or *Eurya* . . . " (p. 289). He later stated (p. 350) without further elaboration that: "*Franklinia* and a few species of *Gordonia* and *Laplacea* possess stellate hairs."

Godfrey and Wooten's description (1981) of pubescence on abaxial leaf surfaces of *G. lasianthus* (Fig. 1) prompted this survey of trichomes and, incidentally, stomatal patterns in the species. A study of related taxa is underway.

MATERIALS AND METHODS

Live plants were collected from 13 counties in Florida and one each in North Carolina and South Carolina. Some materials were supplied by C .A. Aulbach-Smith, R. K. Godfrey, D. W. Hall, J. B. Nelson, T. Nifong, and

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A. G. Shuey; their help is appreciated. Herbarium specimens were examined from other areas. Vouchers are filed at FSU.

Fresh plant tissues were used for observation with the scanning electron microscope (SEM). Abaxial surfaces of flower parts and leaves were studied in addition to twig and petiole surfaces. Suitable portions were vacuum

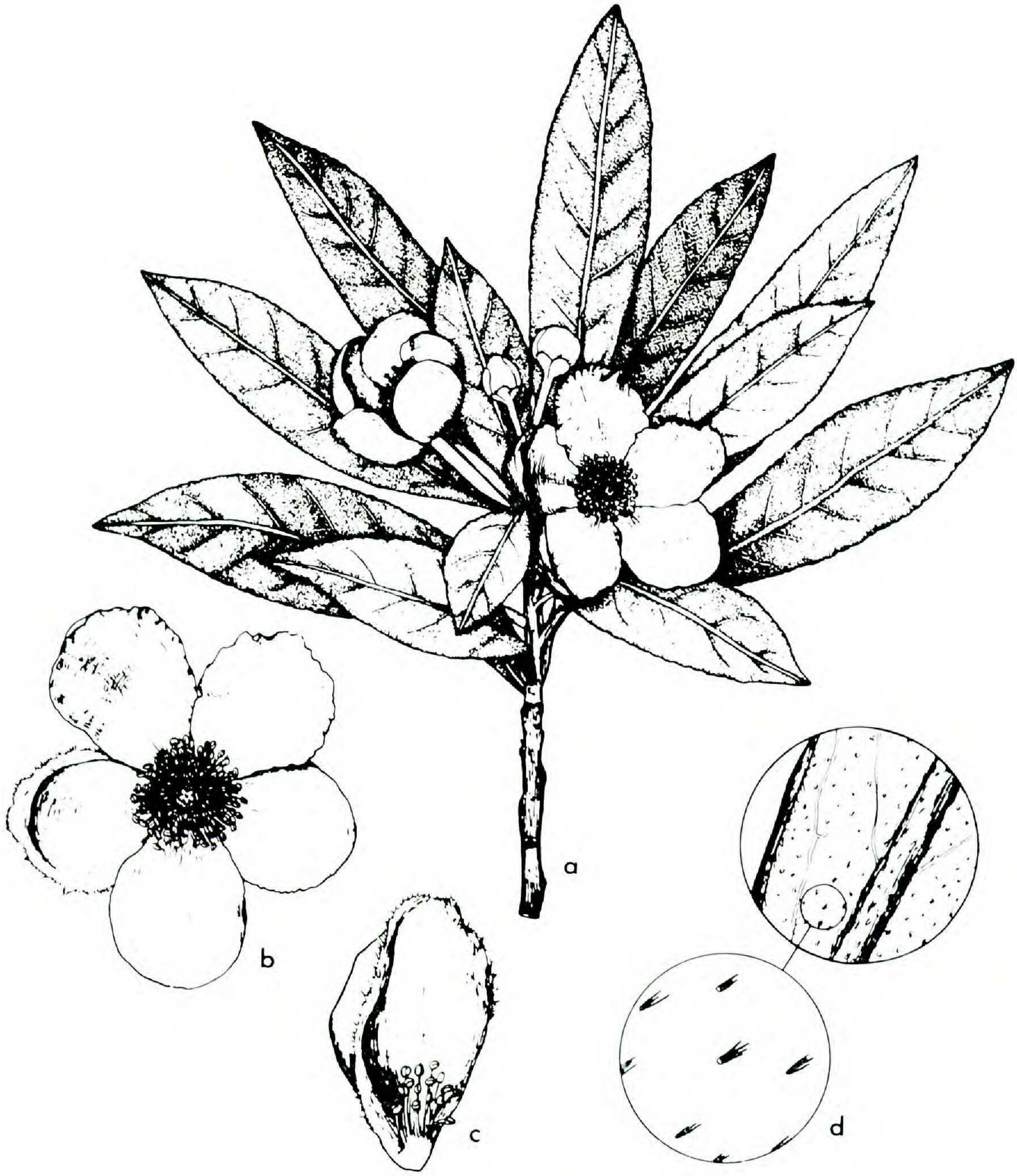

Fig. 1. *Gordonia lasianthus*: a. flowering branch; b. flower, face view; c. petal with one lobe of staminal cup appressed to the base; d. portion of abaxial leaf surface with enlargement of smaller portion showing pubescence.

dried, then sputter coated with 100–200 Å of AuPd (60/40). SEM micrographs were taken on a Cambridge Stereoscan S4-10 at 10–20 keV.

Delicate plant parts are usually prepared for SEM study by critical-point drying. The quicker technique employed here is possible because of the leaf texture and gives equally fine results. Trichome and stomatal measurements were made from epidermal peels (Duco cement imprints) of leaf surfaces. The epidermal peels, from fresh leaf surfaces, confirmed that no artifacts were introduced by the drying and coating processes used for SEM study.

Preserved leaves were embedded, sectioned, and stained through standard microtechniques. Floral parts had to be partially dissected for study because of trichome densities. Average trichome lengths (i.e., mean longest trichomes) were determined from measurements of the longest hairs in over 150 fascicles; individual hairs of the fascicle are nearly equal in length in all instances, so measuring the longest is suitable for comparison. From 50 to 100 measurements were taken to determine averages of other features listed in the tables. Stomatal terminology follows Wilkinson (1979).

RESULTS

TRICHOMES. The most noticeable pubescence in terms of trichome abundance and length occurs on the flowers (Table 1). Sepals (Fig. 2) have prominent ciliate margins with smaller hairs on mid regions of the abaxial surfaces; they are less numerous toward the sepal base. Adaxial and basal abaxial surfaces are glabrous.

Corolla aestivation is imbricate. Trichome abundance and distribution are related to petal position in the bud. The outermost petal has a prominent, continuous marginal fringe like that of the sepals, but the trichomes are usually longer. The abaxial surface of the outermost petal is covered with shorter hairs (Fig. 3). On the inner petals, hairs occur less abundantly and on the basal portions of the petals (areas less likely to be covered by the outer petals in bud). Sclereid distribution within the petals follows trichome patterns on the surface; i.e., if trichomes are restricted to the basal portion of the petal then the sclereids are also.

The staments are glabrous. The ovary is uniformly covered with a dense coat of hairs (similar to those in Fig. 3 but straighter), and the stigma is glabrous. Floral trichomes are single-celled and occur individually or more commonly in fascicles of two, three, or four. Average lengths of floral trichomes are given for selected collections in Table 1.

Most mature branches of *Gordonia lasianthus* are glabrous; younger twigs may have some pubescence near the petioles. Only two patches of scurfy hairs were found on older branches that were otherwise glabrous. In *Anderson 5338* (Fig. 4), the hair fascicles are closely appressed to the twig, whereas in *Aulbach-Smith 1506* (Fig. 5), the hairs of the fascicles are more erect and divergent.

Table 1. Mean trichome lengths (μm) on flower parts of *Gordonia lasianthus*.

Locality and collection	SEPAL sepal margin	SEPAL abaxial side	PETAL petal margin	PETAL abaxial side	ovary surface
Gadsden Co., FL					
Anderson 5976	682.5	255.7	975.7	347.6	477.3
Anderson 5977	711.1	203.3	921.6	290.2	445.5
Leon Co., FL					
Anderson 5338	480.0	288.0	857.9	209.1	475.4
Colleton Co., SC					
Aulbach-Smith 1506	858.7	294.2	553.6	176.8	451.2

Petioles are very short in the loblolly bay and usually have a few black scurfy hairs, as viewed with a hand lens. Extreme examples are covered with hairs that lie flat on the surface (Fig. 6).

Leaf blades are glabrous adaxially, but all that have been examined have fascicled hairs on the abaxial surfaces; these are generally directed toward the leaf tip (Fig. 1-d, 7). The hairs are short, transparent, and often unobserved under a hand lens unless the light angle is favorable. The hairs are thick-walled and strongly birefringent under polarized light; however, cleared whole mounts of leaves are not conducive to study of hairs because of the abundance of idioblastic, branched sclereids in the mesophyll. Hairs are precocious and, therefore, more crowded on developing leaves (Fig. 8). Immature hairs are often crooked (Fig. 8) and partially collapsed (because of SEM vacuum). Mature hairs are mostly straight with smooth, firm surfaces; a few samples were observed with wax depositions on the hairs in the form of warty or crustose flakes. Members of a fascicle are nearly always unequal in length but more or less parallel (Fig. 10–13); only rarely are they widely spreading.

Data of fascicle composition, abundance, and size are given in Table 2. Intraplant measurements came from separate leaves of the same plant and intrapopulation measurements from separate but adjacent plants. Collections in each category are listed by increasing trichome density.

The fascicles are appressed (Fig. 7) and contain two to seven individual hairs (Fig. 8–13) with two and four being the most abundant groupings. Rarely, single hairs are found. Average fascicle density on mature leaves ranges from 2.38 to 7.45 fascicles per mm^2. Mean foliar trichome lengths ranged from 109.5 to 210.4 μm, whereas individual extremes were 57.6 and 432.0 μm long.

STOMATA. Composition of the stomatal apparatus is not observable from surface views (SEM or epidermal peels) because it is hidden by heavy

Fig. 2–7. SEM micrographs with tip of organ to right. 2. Sepal tip, *Anderson 5338*, 40X. 3. Petal near tip, *Anderson 5338*, 280X. 4. Twig with appressed, arachnoid fascicles, *Anderson 5338*, 240X. 5. Twig with ascending fascicles, *Aulbach-Smith 1506*, 240X. 6. Abaxial petiolar region with tightly packed, appressed fascicles, *Aulbach-Smith 1506*, 335X. 7. Leaf surface, low oblique view (30°) showing appressed nature of four-celled fascicle of hairs and cuticular relief, *Hall 610*, 520X.

cuticular relief. Sectioned material reveals the stomatal guard cells are raised and rest upon the subsidiary cells (Fig. 14). Most stomata are cyclocytic with three subsidiary cells (tricytic) surrounding the guard cells (Fig. 15).

Table 2. Means for abaxial leaf surface features of *Gordonia lasianthus*.

Locality and collection	Faccicles per mm^2	Trichomes per fascicle	Trichome length, μm	Stomata per mm^2
INTRAPLANT				
Wakulla Co., FL				
Anderson 5822-1	3.76	2.63	163.4	281.1
Anderson 5822-2	4.11	2.65	136.5	290.9
Anderson 5822-3	4.25	2.73	201.5	312.8
INTRAPOPULATION				
Pender Co., NC				
Anderson 5728	2.42	3.37	115.3	457.6
Anderson 5727	2.44	3.02	169.4	405.3
Gadsden Co., FL				
Anderson 5755	4.97	2.22	145.7	295.7
Anderson 5757	5.12	2.19	146.4	304.2
Anderson 5758	5.16	2.38	129.8	312.8
Anderson 5756	5.24	2.13	136.2	322.5
INTERPOPULATION				
DeSoto Co., FL				
Anderson 5827	2.38	2.38	174.9	279.9
Volusia Co., FL				
Godffrey 78768	2.76	2.38	137.5	316.4
Clay Co., FL				
Anderson 5710	3.07	2.21	148.2	290.0
Jefferson Co., FL				
Nelson 2024	3.39	2.72	115.5	283.6
Franklin Co., FL				
Anderson 5821	3.76	2.32	137.6	262.9
Hardee Co., FL				
Anderson 5826	4.30	3.30	109.5	322.5
Alachua Co., FL				
Hall 610	4.88	2.29	136.8	378.5
Liberty Co., FL				
Anderson 5769	4.94	2.08	138.9	318.9
Manatee Co., FL				
Anderson 5825	4.99	3.35	210.4	334.7
Colleton Co., SC				
Albach-Smith 1506	5.23	2.80	176.2	390.7
Leon Co., FL				
Anderson 5338	5.25	2.32	159.6	367.5
Hillsborough Co., FL				
Anderson 5824	7.45	3.27	138-1	205.7

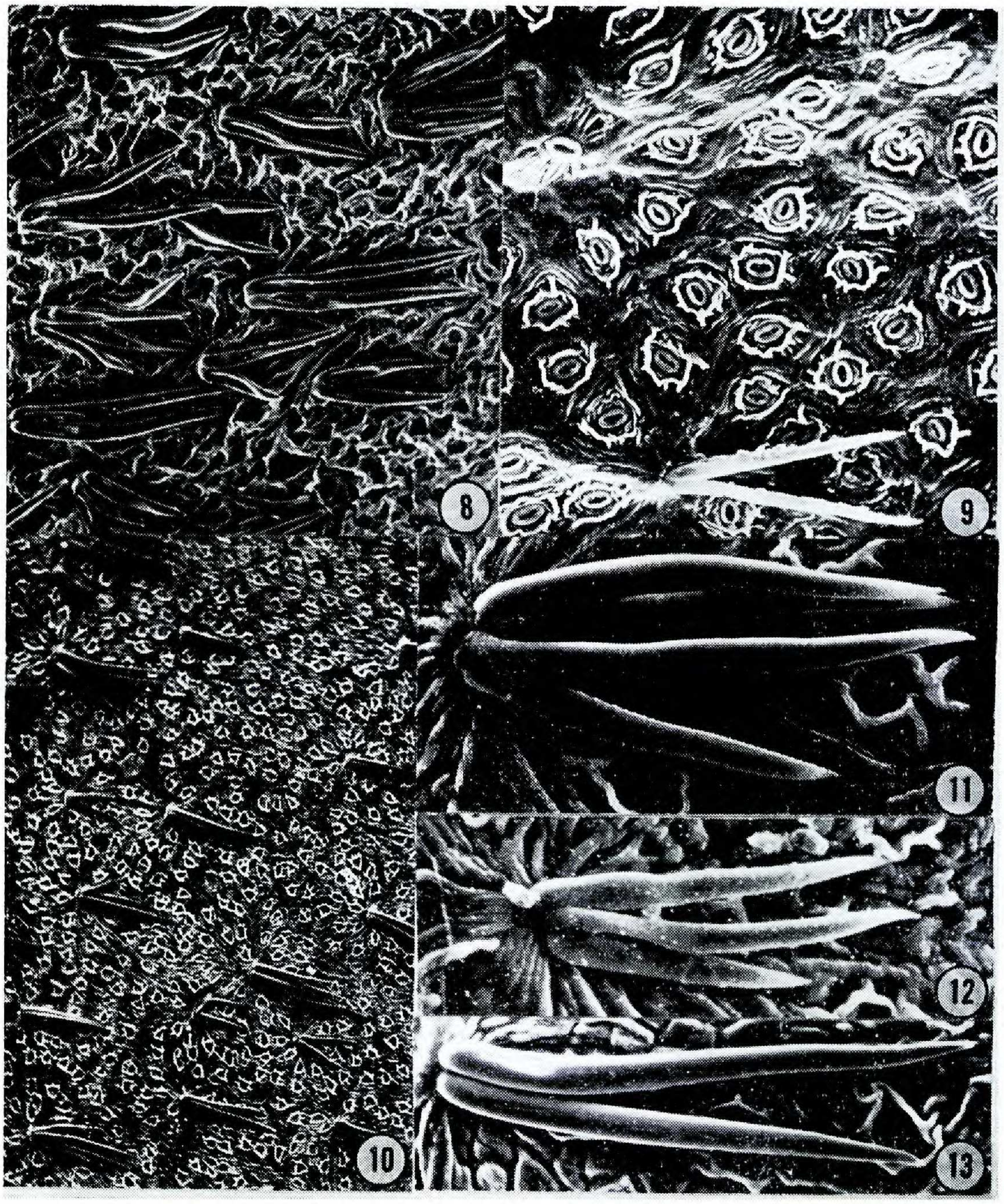

Fig. 8–13. SEM of foliar trichomes, leaf tip to the right. 8. Young leaf surface showing precocious trichomes not yet turgid and straight; stomata and cuticular patterns not fully developed, *Anderson 5759*, 250X. 9. Trichome bifurcate, primary stoma at upper left, *Anderson 5769*, 250X. 10. Mature leaf surface showing trichome fascicles and stomata, *Hall 610*, 70X. 11. Trichome with four cells in the fascicle, *Aulbach-Smith 1506*, 520X. 12. Trichome with three cells in the fascicle, *Anderson 5710*, 520X. 13. Trichome with two cells in the fascicle (bifurcate), *Hall 610*, 520X.

The subsidiary cells stain differentially in fast green-orange G combinations; they stain light green, whereas non-stomatal cells of the epidermis stain orange.

Average guard cell length for *Anderson 5338* is 26.5 μm; that of primary or giant stomata averages 31.2 μm. Stomatal size can be measured only in sectioned material and, therefore, is not listed in Table 2 for other collections; however, stomatal densities from epidermal peels are given. Stomata are distinguishable by more than size differences. The standard stomata have three subsidiary cells that are periclinally oriented around the guard cells. Primary stomata have eight subsidiary cells (octocytic) that are larger and anticlinally oriented around the guard cells. The two size classes of stomata are further distinguished by cuticular patterns (see below).

Although stomata appear raised in sectioned material, they appear sunken in SEM surface view because of the cuticular patterns. The stomatal rims are raised into prominent funnel-like structures with long, narrow apertures that nearly hide the guard cells (Fig. 16–20). Stomatal rims are often finely reticulate rather than being smooth. In addition, their inner walls may be undulate or flat (Fig. 18).

The peristomatal rim or ridge is usually raised into a high buttressed cup (Fig. 9, 16). Oblique SEM views show the buttressing and height of the cup more clearly (Fig. 18). Of the populations studied, all but two have the peristomatal cup. Leaves of a population from Gadsden County, Florida, have concentric rings of peristomatal striae rather than the buttressed cup (Fig. 19–20). Five sampled trees all have these cuticular striations. *Anderson 4314* (Fig. 20) was the first sample of *Gordonia* observed in this study; data for the other four are listed in Table 2. One sample, *Anderson 5821*, taken from a tree in Franklin County, Florida, also has the peristomatal striae.

Primary or giant stomata on all samples have cuticular striations (Fig. 9, 17) rather than buttressed cups. The striae are not as abundant as in the Gadsden and Franklin County plants, but they extend into raised ridges at the ends of the stomata.

Fig. 14–20. Light and electron micrographs of stomatal features. 14. Leaf transection showing guard cells raised on supporting subsidiary cells of lower epidermis with portion of large idioblastic sclereid to the left, *Anderson 5338*, 300X. 15. SEM of paradermal section showing standard stomata each with three subsidiary cells (tricytic), *Anderson 5338*, 500X. 16. Stomata with prominent stomatal rims nearly hiding guard cells, peristomatal rims as buttressed cups, *Godfrey 78768*, 500X. 17. Primary or giant stoma with stomatal rim flanked by cuticular striae that extend as ridges from ends of the stoma, *Anderson 5728*, 500X. 18. High oblique view (60°) showing fine reticulum on two of the stomatal rims plus height and buttressing of peristomatal cups, *Anderson 5710*, 1000X. 19. Sample from Gadsden County without peristomatal ridges or cups with numerous cuticular striations surrounding each stoma and smooth interstitial cuticle, *Anderson 5756*, 500X. 20. Trichome and stomata from Gadsden County sample, note fugal hypha (frequent on some samples), *Anderson 4314*, 500X.

A final aspect of cuticular variation amongst the populations relates to the interstomatal surface. The cuticle may be relatively smooth (Fig. 19–20), rugose with interstitial epidermal walls apparent (partially seen in Fig. 13),

raised into striations between buttressed cups (Fig. 16), or raised into irregularly rounded or warty plateaus (Fig. 18).

DISCUSSION

Abaxial leaf hairs appear to be universal for the species, and the peristomatal cups are widespread. Only two populations from Gadsden and Franklin Counties, Florida, have been found that have peristomatal cuticular striae rather than buttressed cups. Recent surveys show additional Gadsden County populations (those in Table 1) possess the standard buttressed cup.

Correlations among features listed in Table 2 are not clearly indicated. One might expect trichome density to be negatively correlated with stomatal density. The two samples from North Carolina do have relatively low trichome densities and high stomatal densities, and the converse is true for the sample from Hillsborough County, Florida. But several exceptions can be seen; i.e., the DeSoto County, Florida, plant has the lowest trichome density and relatively low stomatal density, and the reverse correlation is found in samples from Leon County, Florida, and South Carolina.

Keng (1962) designated stomata in the Theaceae that had subsidiary cells as the "gordoniaceous type" and noted that, with few exceptions such as *Franklinia*, they generally characterized the subfamily Camellioideae. He illustrated tricytic stomata for species of *Hartia* and *Schima*, but he did not record the octocytic type found here in the primary stomata of *Gordonia lasianthus*.

My preliminary survey of related taxa reveals the fascicled trichomes are absent in 11 Asian species of *Gordonia*; single-haired trichomes are found on leaves of *G. axillaris, G. chrysandra, G. elliptica, G. obtusa,* and *G. penangensis,* whereas leaves of *G. balansae, G. luzonica, G. papuana, G. speciosa, G. welbournei,* and *G. zeylanica* are glabrous. The Asian species also appear to lack buttressed peristomatal cups, but SEM study of air-dried material is problematic because of artifacts in the cuticular pattern.

Of 17 species of *Laplacea* examined, leaves of *L. fruticosa* have bifurcate trichomes, those of *L. grandis* are stellate, and those of *L. acutifolia, L. alpestris, L. angustifolia, L. ceurtoensis, L. curtyana, L. haematoxylon, L. moaensis, L. obovata, L. portoricensis, L. reticularis,* and *L. tomentosa* have single-haired trichomes. Leaves of *L. cymatoneura, L. semiserrata,* and *L. speciosa* are glabrous. Recently, Keng (1980) merged the genus *Laplacea* into *Gordonia.*

Three species of the nine seen in *Schima* have bifurcate trichomes on abaxial leaf surfaces (*S. argentea, S. khasiana,* and *S. wallichii*), whereas leaves of *S. mertensiana* and *S. superba* have single-haired trichomes. Leaves of *S. confertiflora, S. crenata, S. noronhae,* and *S. sinensis* are glabrous. Buttressed stomata were not observed in *Schima.* Bloembergen (1952) considers *Schima* monotypic with *S. wallichii* having several subspecies. Cer-

tainly a more detailed study of variation, including foliar trichomes, is warranted for *Schima.*

Trichomes and stomata on leaves of *Stewartia* and *Franklinia* differ markedly from those of *Gordinia lasianthus. Stewartia* has numerous, uniseriate trichomes, and *Franklinia* has a mixture of single, bifurcate, and stellate hairs. Contrary to Keng's statements (1962), foliar stellate hairs were not observed on any species of *Gordonia* (sens. strict.) in my study, but fascicled trichomes do occur in *G. lasianthus.*

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