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VEGETATIVE MORPHOLOGY AND LEAF ANATOMY OF *CATOPSIS* (TILLANDSIOIDEAE: BROMELIACEAE)

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ABSTRACT. Members of *Catopsis* were examined for taxonomically useful morphological and anatomical characteristics related to leaves. External features included rosette shape, leaf size and shape, presence of epicuticular wax, abundance and character of trichomes, and ratio of trichomes to stomata. Leaf anatomical characters included arrangement of stomatal-complex cells, thickness of water storage tissue, and features of the vascular bundle sheath. In general, leaf morphology and anatomy were found to be similar across all species of *Catopsis*. A number of the characters are associated with habitat preference and thus presumed to be of ecological and ecophysiological significance, but of little taxonomic value.

Key words: ecology, epicuticular wax, peltate trichome, stoma/trichome ratio, water storage tissue

INTRODUCTION

The species of *Catopsis* Griseb. are mostly obligate epiphytes and, as such, exhibit specific morphological adaptations for life in the canopy. The presence of a water-impounding rosette, or phytotelm, minute water-absorbing scales, holdfast roots, and the specialized seed appendage with terminal hooks are examples of these adaptations. A few populations of *C. floribunda* L.B. Sm. have been found growing on rocks, but this seems to be a rare, occasional situation.

Within the Tillandsioideae, few, if any, vegetative features are unique to *Catopsis*. Consequently, sterile plants are not easily distinguished from similar tank-forming species of *Guzmania* Ruiz & Pav., *Tillandsia* L., or *Vriesea* Lindl. in the field. *Catopsis* specimens, however, often can be recognized by a suite of characters including shiny green leaves, usually with a distinct hyaline margin, and frequently a white (i.e., cretaceous) coating, or bloom of conspicuous epicuticular waxes (Smith & Downs 1977).

Taxonomically, leaf variation and rosette morphology have been used as diagnostic characters to differentiate among *Catopsis* species (Mez 1935, Smith & Downs 1977). In addition, variation in foliar trichomes and associated micromorphological features have been judged to be of taxonomic value in several genera of the Bromeliaceae, e.g., *Tillandsia, Pitcairnia,* and *Aechmea* (Tomlinson 1969, Strehl & Winkler 1981, Gardner 1983, Varadarajan & Gilmartin 1987, Beaman & Judd 1996, Silva 2003). Except for the general correlation between leaf margin type and the three recognized subfamilies, however, the vegetative features of the Bromeliaceae seem to be associated more with ecological and ecophysiological adaptations than with genetic and taxonomically useful variation (Tomlinson 1969, Benzing 1976, Palací & Brown 1994). Variation in rosette type, leaf shape and size, and leaf anatomical features of *Catopsis* species are discussed in the following sections. The ecological and ecophysiological significance of the different morphological features is emphasized and the taxonomic relevance is discussed.

METHODS AND MATERIALS

Leaf materials were obtained from species collected in Costa Rica and Guatemala in September 1993 and from cultivated specimens obtained from the Marie Selby Botanical Gardens, Sarasota, Florida (SEL), Denver Botanical Gardens, Denver, Colorado (DBG), Heidelberg University Botanical Gardens, Heidelberg, Germany (HEIL), and the Williams Conservatory, University of Wyoming (UWWC). Additional material was obtained from selected non-type herbarium specimens with permission from the corresponding herbaria. Free-hand sections for leaf anatomy were made from living specimens and mounted in 2–3 drops of Hoyer's solution previously mixed with 1–2 drops of toluidine-blue-O and one drop of 1% safranin-O. Stained leaf sections were observed and photographed using phase-contrast microscopy. For scanning electron microscopy (SEM), leaf samples were fixed in 3% gluteraldehyde for at least 24 hours, followed by a thorough rinse in distilled water just prior to a modified OTO-treatment (1% osmium tetroxide; saturated thiocarbohydrazide; 1% osmium tetroxide; Postek & Tucker 1977). Samples were then progressively dehydrated to

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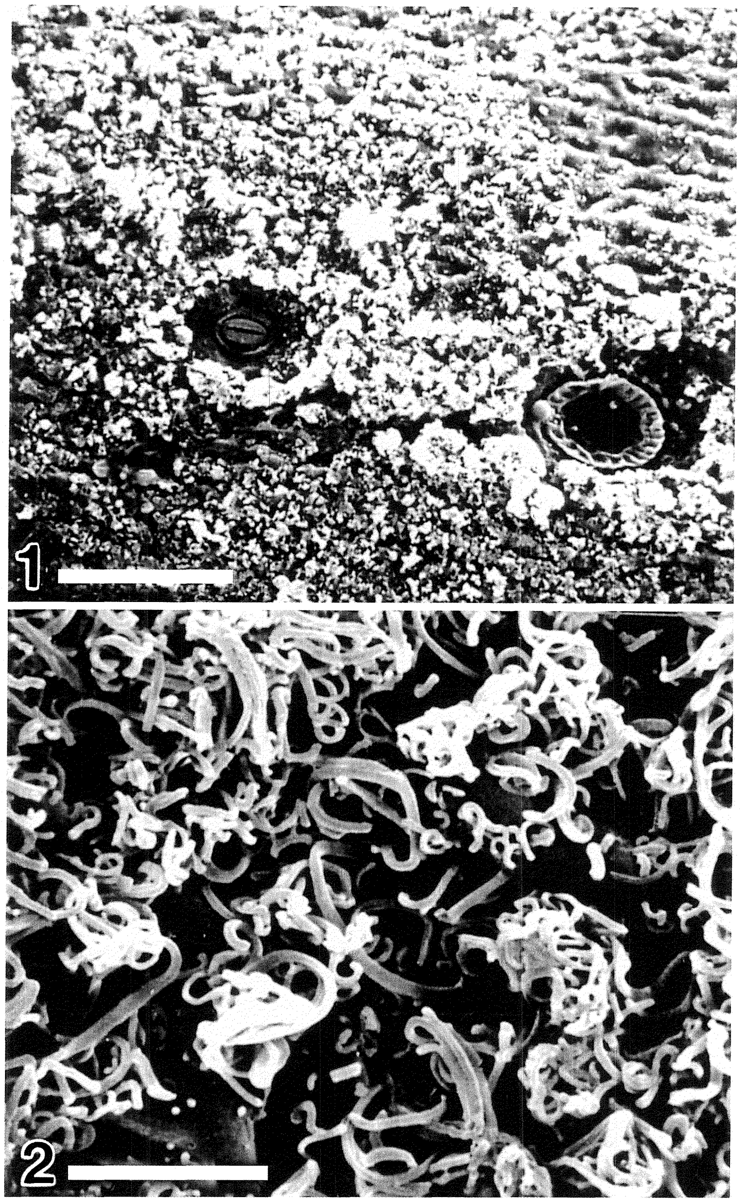

FIGURE 1. Scanning electron photographs of epicuticular waxes on leaves of *Catopsis* (source plant). **1.1.** Abaxial surface of *C. berteroniana* (DBG 6772197). One stomatal complex (left) and one peltate trichome (right) are visible. Bar = 100 μm. **1.2.** *C. morreniana* (DBG 772186). Higher magnification of the "*Strelizia* Type" of epicuticular wax. Bar = 10 μm.

100% ethanol, critical point dried, mounted on aluminum stubs and sputter-coated with gold, following Brown and Gilmartin (1989). Leaf sections were observed using a JEOL JSM-35C scanning electron microscope and photographs captured from a computer graphics screen using 35 mm black and white film.

RESULTS AND DISCUSSION

Based on general characteristics, two basic leaf types can be recognized among species of *Catopsis.* The leaves of *C. juncifolia* Mez & Wercklé ex Mez and *C. floribunda,* for example, exhibit narrowly triangular blades with relatively narrow sheaths forming a tight rosette with limited capacity for impounding water. These species represent the semi-mesic type of Gilmartin (1983) and Gilmartin and Brown (1986). Most *Catopsis* species, however, have broad, ligulate leaves with broadly expanded sheaths forming a large water-impounding tank, representative of the mesic type (Gilmartin 1983, Gilmartin & Brown 1986). Examples include *C. paniculata* E.Morren s.l., *C. nitida* (Hook.) Griseb., and *C. nutans* (Sw.) Griseb. Species of the semi-mesic type have thicker water-storage tissue (WST) and relatively high trichome density. In contrast, mesic type species have thinner leaf blades with poorly developed WST and lower trichome density (see below). Despite the continuum between these two ecological types, this general classification may be useful for future ecological work involving *Catopsis.*

The leaves of *Catopsis* are simple, entire, rosulate, with inconspicuous, sparsely distributed, appressed peltate trichomes. Leaf length, including the sheath, ranges from 9–56 cm for all known species. Variation exists in the leaf shape and arrangement among the different species, and both leaf shape and size tend to vary among pistillate, staminate, and perfect forms of the same species and also between plants from different locales. For example, the leaves of *C. sessiliflora* (Ruiz & Pav.) Mez are typically ligulate with acute to rounded apices and terminated with a distinct mucronate tip. In contrast, pistillate plants of the same species from Mexico exhibit acuminate leaves with short caudate or acuminate apices, thus resembling those of *C. nutans.* Furthermore, a similar dimorphism occasionally can be observed in different leaves from a single *C. nutans* plant. Given the qualitative variability seen in leaf shape and sizes, a quantitative assessment of leaf characteristics was conducted to evaluate species circumscriptions in the genus (C. Palací, G. Brown, and D. Tuthill unpubl. data).

The leaves of most species of *Catopsis* are typically arranged into a lax rosette containing moderate amounts of water (i.e., tank-epiphytes). The expanded sheaths of *C. subulata* L.B. Sm., and to a lesser extent those of *C. wangerinii* Mez & Wercklé ex Mez and *C. pisiformis* Rauh, result in the formation of a broader, globose to subglobose rosette impounding comparatively larger amounts of water. The water-impounding rosette reaches its maximum expression in *C. nitida,* in which the leaves form a closed, tubular rosette. The tubular rosette of this species closely resembles that of *Brocchinia reducta* Baker (subfamily Pitcairnioideae), in which carnivory has been indicated (Givnish et al. 1984).

The presence of a waxy bloom on the leaves is a feature frequently observed in *Catopsis.* At high magnification, these epicuticular waxes appear as massive, rod-like projections over extensive areas of the leaf surface, especially abaxially and towards the base, giving a cretaceous-coated appearance to the leaf (FIGURE 1). This particular type of wax deposition, characterized as the "*Strelitzia* Type," appears to be restricted to four monocot orders (Zingiberales, Poales, Pandanales, and Arecales), thus providing some taxonomic utility at the superorder level (Barthlott & Frölich 1983, Chase et al. 2000). In the Bromeliaceae, the presence of foliar wax blooms has been used as a secondary diagnostic character to differentiate *Catopsis* from other members of the Tillandsioideae (Smith & Downs

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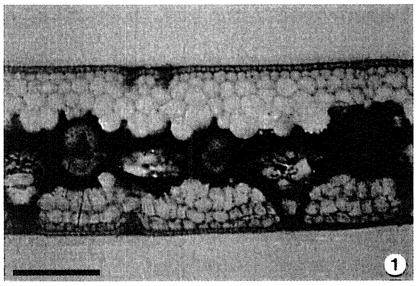
FIGURE 2. Anatomical features of *Catopsis* leaves (source plant). **2.1.** *C. paniculata* (SEL 1981–0250) leaf cross-section, the adaxial surface is the upper surface. Bar = 200 μm. **2.2.** *C. morreniana* (UWWC) leaf cross-section, the adaxial surface is the upper surface. Bar = 200 μm. **2.3.** *C. juncifolia* (SEL 1990-0779) leaf cross-section, the adaxial surface is the upper surface. Bar = 200 μm. **2.4.** *C. floribunda* (Palací 1239, Guatemala) leaf cross-section, the adaxial surface is the upper surface. Bar = 200 μm. **2.5.** *C. paniculata* (SEL 1981-0250) vascular bundle showing the sclerified bundle sheath and presumed ligno-suberized layer between the xylem and phloem. Bar = 50 μm. **2.6.** *C. paniculata* (SEL 1981-0250) leaf cross-section. Adaxial epidermis with thickened inner periclinal cell walls. WST separates the adaxial epidermis from the chlorenchyma tissue. A vascular bundle is visible, located within the chlorenchyma. Bar = 100 μm. **2.7.** *C. floribunda* (Palací 1239) leaf cross-section, the adaxial surface is the upper surface. Detail of water storage tissue. Bar = 100 μm. **2.8.** *C. floribunda* (Palací 1239) stomata complex and surrounding epidermis in periclinal view. Note the undulate nature of the adjacent anticlinal cell walls. Bar = 50 μm. **2.9.** Peltate trichome of *C. floribunda* (Palací 1239). Note the conspicuous uneven thickening of the adjacent wing cell anticlinal walls. Bar = 50 μm. **2.10.** Peltate trichome of *C. nutans* (Tropiflora S.N., Costa Rica) with uniformly thin anticlinal walls between adjacent wing cells of the cap. Bar = 50 μm. **2.11.** Epidermis of *C. sessiliflora* (UWWC), example of a relatively high stomata/trichome ratio. Trichomes stain dark. Bar = 200 μm. **2.12.** Epidermis of *C. paniculata* (SEL 1981-0250), example of a more intermediate stomata/trichomes ratio. Trichomes stain dark. Bar = 200 μm. **2.13.** Epidermis of *C. floribunda* (Palací 1239), example of a somewhat lower stomata/trichome ratio. Trichomes stain dark. Bar = 200μm.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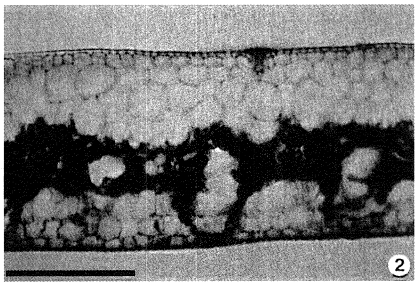
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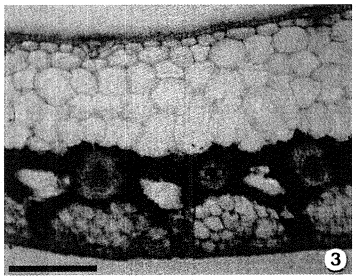
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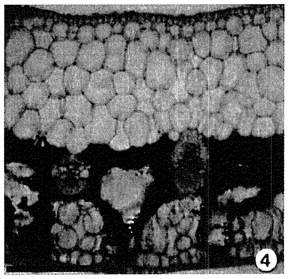
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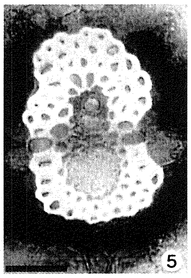
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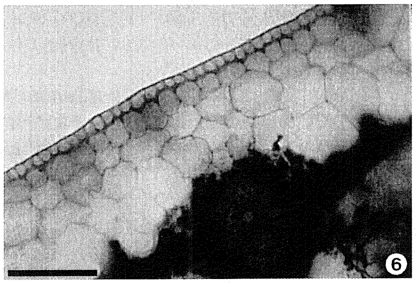
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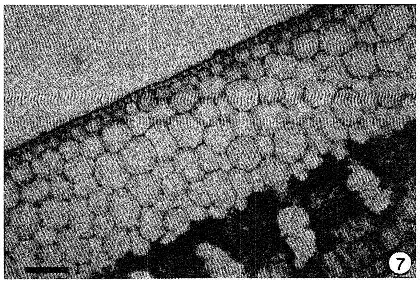
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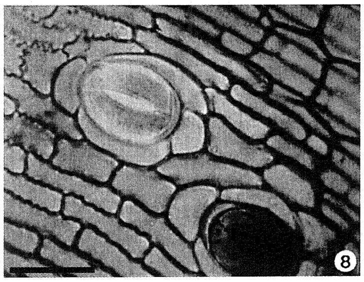
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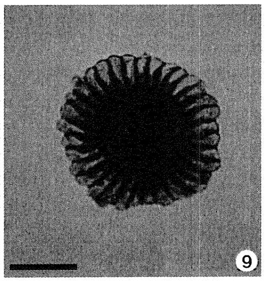
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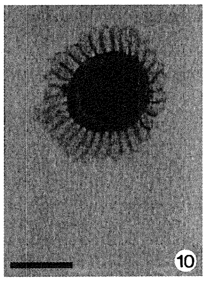
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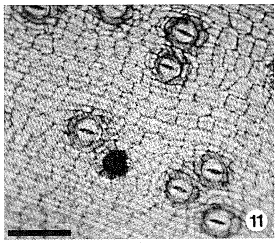
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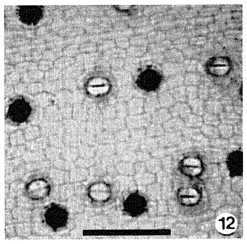
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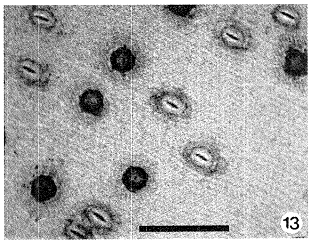
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1977: 665), although two species of *Catopsis* actually lack this character (*C. juncifolia* and *C. nitida*). Moreover, species with epicuticular wax blooms are found in other bromeliad genera (e.g., *Aechmea, Brocchinia, Vriesea*).

According to Martin and Juniper (1970), leaf waxes provide a reflective surface that reduces light interception and water loss, especially when in the form of projecting rods or a crystalline or semi-crystalline structure, and have been interpreted as an adaptation to exposed habitats. Plants of *Catopsis* with abundant epicuticular waxes tend to occupy the higher levels in the tree canopy and fully exposed habitats of the forest profile (C. Palací pers. obs.). The hydrophobicity of waxy surfaces may also be beneficial in keeping stomata clear of debris and, more importantly, water, so that gas exchange is not compromised during wet conditions (Pierce et al. 2001). It is possible that the secretion of conspicuous epicuticular waxes is a multi-purpose adaptation to highly exposed habitats, in that it may reduce solar radiation, enhance water impoundment ability, and maintain gas exchange capability.

Epicuticular waxes are also thought to aid in the trapping of insects in *Catopsis berteroniana.* Insects appear to be attracted to the tanks of this species but are unable to escape because of the slick, friable wax layer (FIGURE 1.1, Fish 1976, Frank & O'Meara 1984, Benzing 2000). Furthermore, Fish (1976) speculated that UV light reflected from waxy leaf surfaces is responsible for insect capture, as it confuses insects in flight, causing them to tumble into the impounded water; but this effect has not been confirmed (Benzing 2000). Interestingly, *C. nitida,* the species of *Catopsis* with a tubular rosette most like *Brocchinia reducta,* the only other carnivorous bromeliad, mostly lacks the waxy bloom characteristic of most members of the genus.

Basic leaf anatomical features for the Bromeliaceae have been described by Tomlinson (1969). Generally, the leaves of *Catopsis* exhibit the typical bromeliaceous anatomy with few to no features exclusive to the genus (FIGURES 2, 3). The epidermis is composed of rectangular cells with undulating adjacent anticlinal walls in periclinal (surface) view (FIGURE 2.8). In cross-section, the epidermal cells typically exhibit a marked thickening of the inner periclinal wall, thus appearing U-shaped (FIGURE 2.6). Also, epidermal cells usually contain one to several small, spherical silica bodies. The stomata are positioned at the same level as the surrounding epidermis (FIGURE 3.8), a feature regarded as unspecialized by Tomlinson (1969). Each pair of guard cells is surrounded by six subsidiary cells, corresponding to the hexacytic type of Van Cotthem (1970). The two pairs of subsidiary cells in *Catopsis,* however, are usually in the polar position rather than oriented parallel to the long axis of the guard cells and stoma as described by Van Cotthem (FIGURE 2.8). The adaxial hypodermis is thin-walled and cannot be distinguished from the adjacent WST (FIGURE 2.1–2.4, 2.6, and 2.7). The abaxial hypodermis is also thin-walled and is continuous with the two or three cell layers of hyaline parenchyma that may represent an abaxial WST.

Adaxial water storage tissue, common in bromeliad leaves, is universally present but variable in width in *Catopsis* species. The WST is relatively narrow (2–3 cell layers) in mesic taxa, such as *C. paniculata* (FIGURES 2.1, 2.6, 3.1), *C. morreniana* Mez (FIGURES 2.2, 3.5), *C. nitida* (FIGURE 3.2), *C. sessiliflora* (FIGURE 3.6), and *C. berteroniana* (Schult.f.) Mez (FIGURE 3.7). In contrast, semi-mesic species such as *C. floribunda* and *C. juncifolia* exhibit a well-developed WST of 5–8 cell layers (FIGURES 2.3, 2.4, 3.3, and 3.4), giving the leaves more of a succulent appearance.

The ecophysiological significance of the WST is poorly understood. Medina (1970) observed that bromeliads with C3 photosynthesis have an achlorophyllous WST, whereas plants with CAM photosynthesis typically contain chloroplasts throughout a continuous water-storage parenchyma tissue. In contrast, Loeschen et al. (1993) observed variable development in an achlorophyllous WST in 12 epiphytic species of *Tillandsia,* all with CAM. Martin (1994) hypothesized that the WST, which actively respires but lacks chlorophyll, might contribute extra CO_2 for CO_2 recycling during CAM photosynthesis. Loeschen et al. (1993) specifically tested this hypothesis and found no significant correlation between WST and CO_2 recycling during CAM (see Martin 1994). Additional functions of the WST in light protection and temperature regulation have also been proposed, but little is known on the subject to date (T. Vogelmann pers. comm.).

The chlorenchyma tissue is traversed by typical "air-lacunae" filled with loose, stellate cells that are continuous with the substomatal chambers located below the abaxial epidermis (FIGURES 2.1–2.4). Typically the spongy air-lacunae are conspicuous, alternating with single vascular bundles across the mesophyll (FIGURES 2.1–2.4, 2.7, 3.1, 3.5, and 3.7).

Leaf vascular bundles, surrounded by a conspicuously sclerified sheath, include a layer of thick-walled cells that separates the xylem from the phloem (FIGURE 2.5). Tomlinson (1969: 262) discussed the thick-walled bundle sheath and intra-bundle layers and their presumed ligno-su-

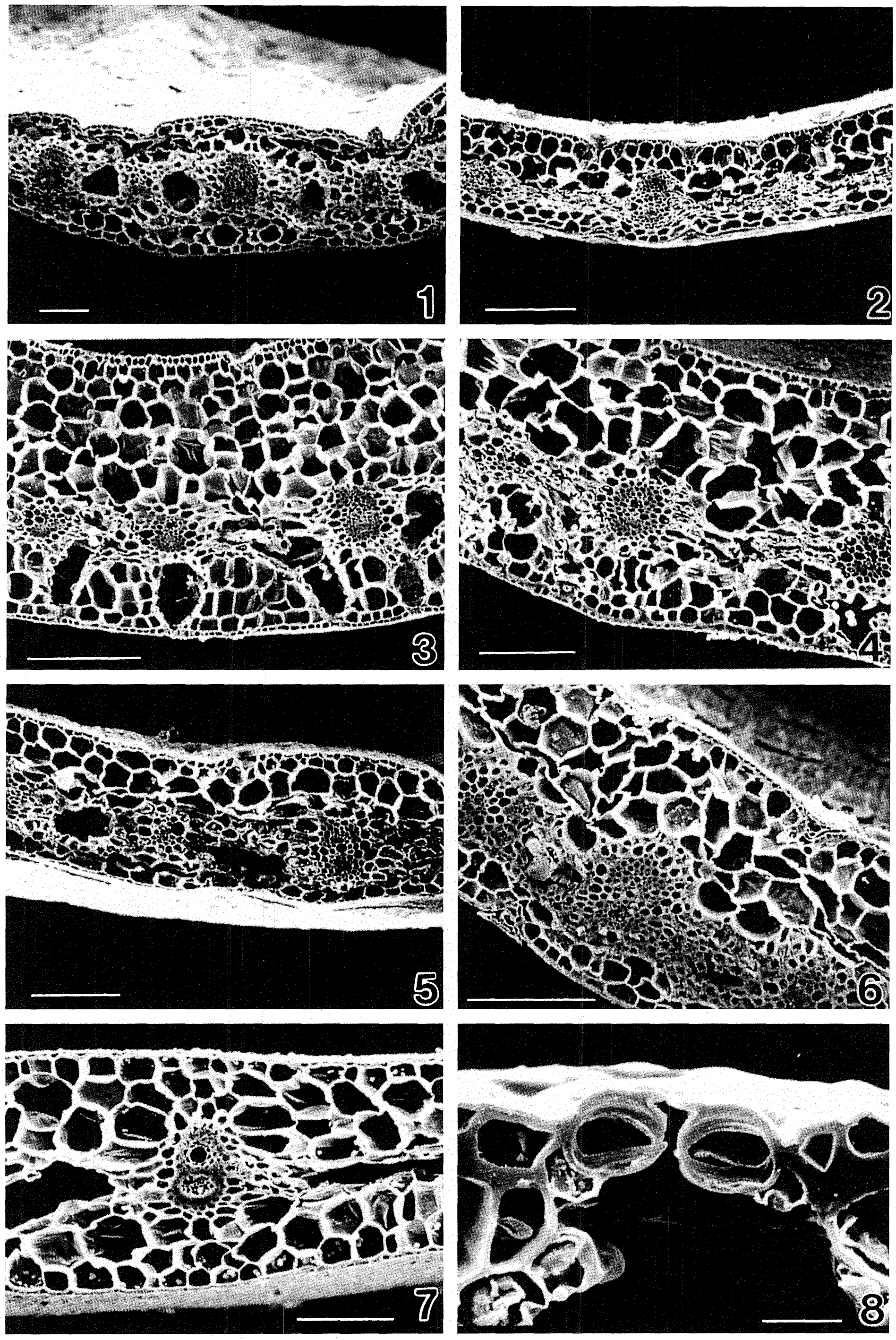

FIGURE 3. SEM photographs of leaf cross-sections of *Catopsis* species. **3.1–3.7.** The upper surface corresponds to the adaxial surface. Bar = 200 μm. **3.1.** *C. paniculata* (ex hort, Tropiflora S.N.). **3.2.** *C. nitida* (Palací 1246). **3.3.** *C. floribunda* (HEIL 44249). **3.4.** *C. juncifolia* (SEL 1990-0779). **3.5.** *C. morreniana* (SEL 1981-0220). **3.6.** *C. sessiliflora* (Palací 1226). **3.7.** *C. berteroniana* (DBG 6772197). **3.8.** *C. paniculata* (Palací 1236) stoma and guard cells in cross-section. Stomatal complex at same level as surrounding epidermis. Bar = 20 μm.

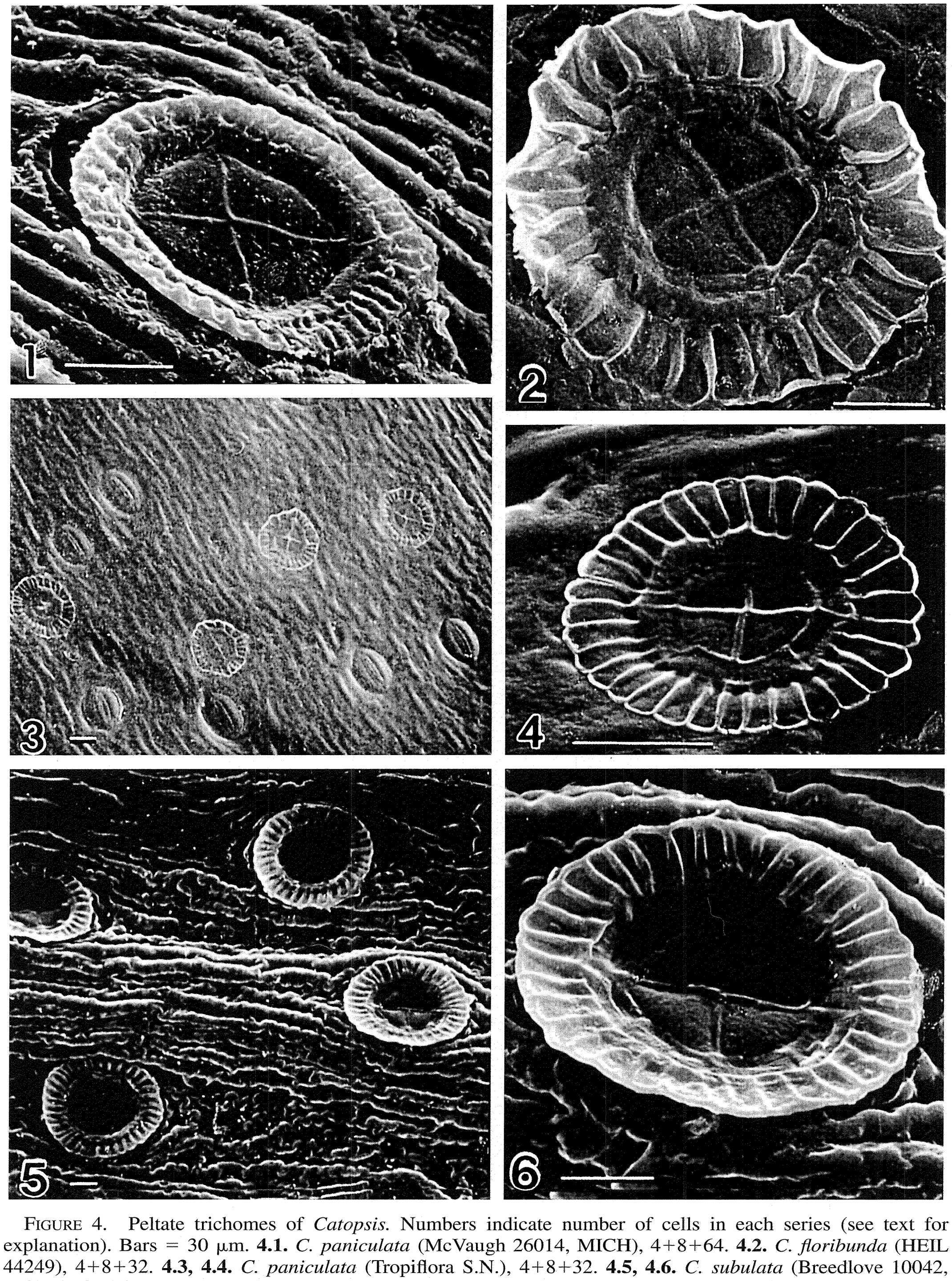

FIGURE 4. Peltate trichomes of *Catopsis*. Numbers indicate number of cells in each series (see text for explanation). Bars = 30 μm. **4.1.** *C. paniculata* (McVaugh 26014, MICH), 4+8+64. **4.2.** *C. floribunda* (HEIL 44249), 4+8+32. **4.3, 4.4.** *C. paniculata* (Tropiflora S.N.), 4+8+32. **4.5, 4.6.** *C. subulata* (Breedlove 10042, MO), 4+8+36.

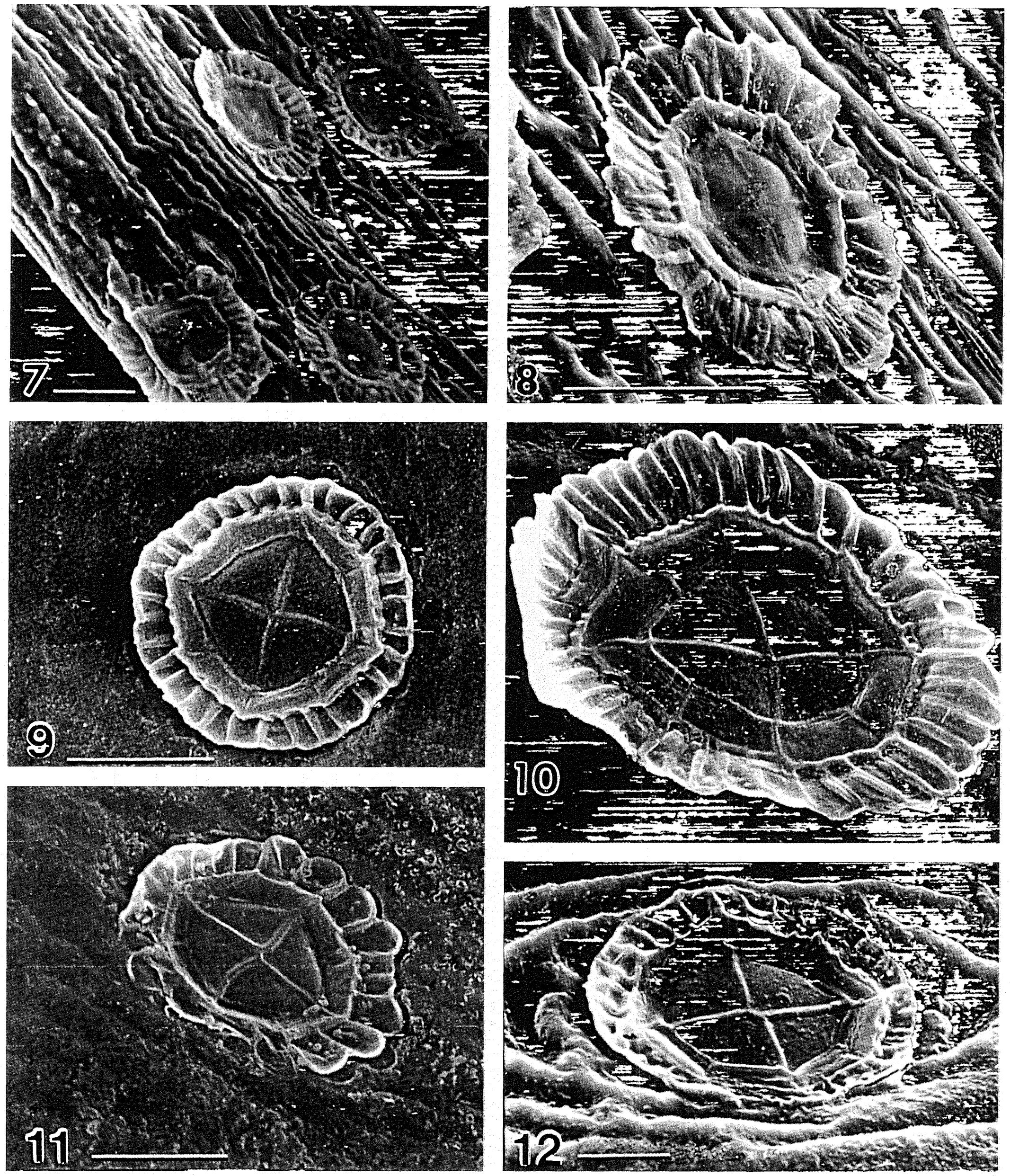

FIGURE 4. (Continued) **4.7, 4.8.** *C. juncifolia* (SEL 1990-0779), 4+8+34. **4.9.** *C. montana* (Gilmartin 3979), 4+8+32. **4.10.** *C. minimiflora* (HEIL 36407), 4+8+44. **4.11.** *C. morreniana* (SEL 1981-0230), 4+8+24. **4.12.** *C. compacta* (Zona S. 233, XAL), 4+8+32.

berized status and putative endodermal function and suggested that this might be distinctive for the Tillandsioideae.

Robinson (1969) investigated the anatomical features of 102 species in the genera *Connellia* N.E.Br., *Cottendorfia* Schult.f., and *Navia* Mart. ex Schult.f. (all Pitcairnioideae) and found that most species could be distinguished on the basis of vegetative characters. In contrast, species of *Catopsis* exhibit rather homogeneous anatomical features with little apparent taxonomic utility. Anatomical differences, however, appear to have potential importance from an ecological and ecophysiological point of view.

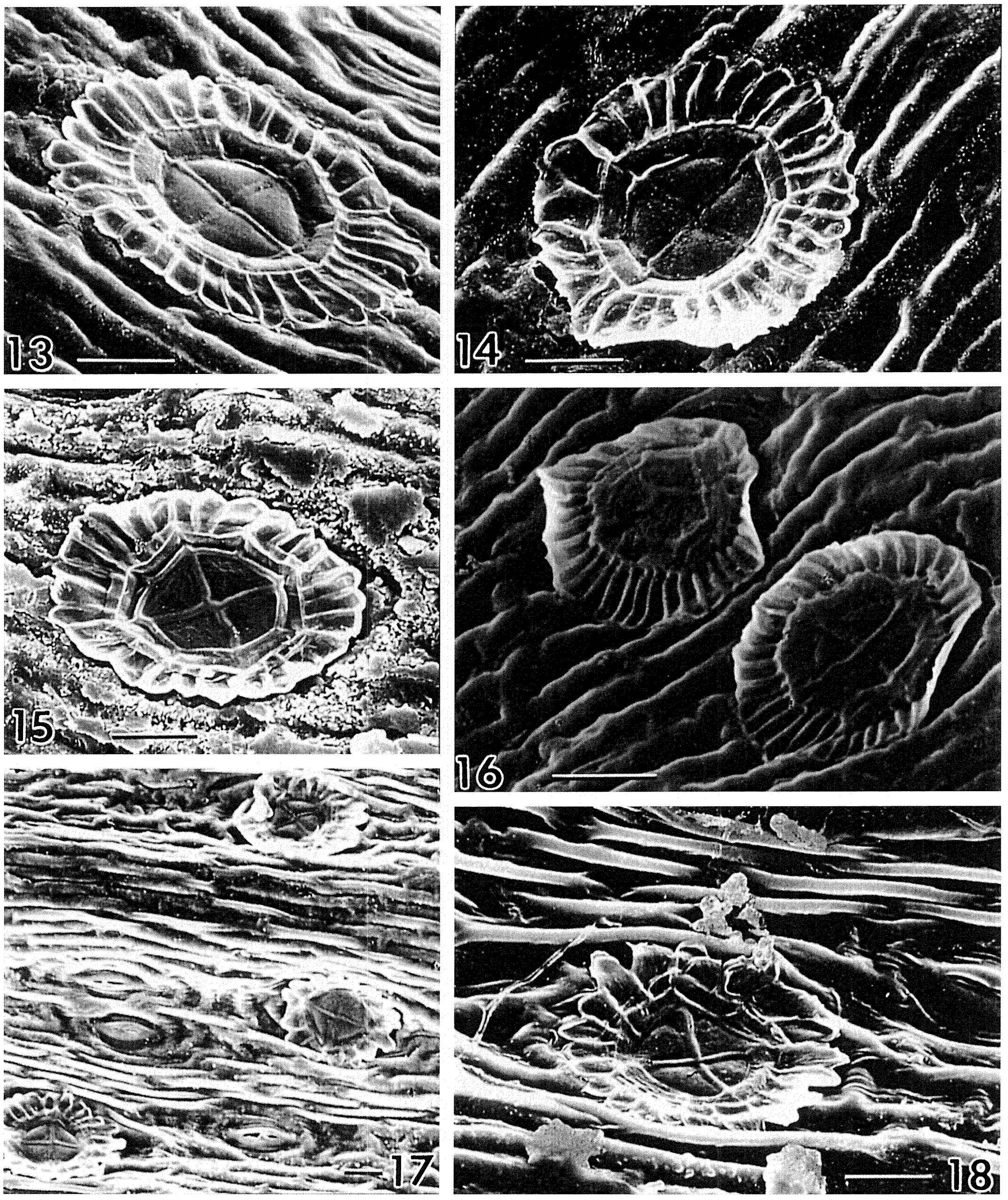

FIGURE 4. (Continued) **4.13.** *C. nutans* (SEL 1976-2058), 4+8+32. **4.14.** *C. nutans* (SEL 1976-2058), 4+8+30. **4.15.** *C. sessiliflora* (Palací 1226), 4+8+30. **4.16.** *C. nitida* (Palací 1246), 4+8+32. **4.17, 4.18.** *C. delicatula* (Palací 1241), 4+8+20.

The specialized peltate trichomes, or leaf scales, of the Bromeliaceae have been the subject of numerous investigations since their first description by Rudolphy in 1807 (see Brown 1972). According to Gilmartin and Brown (1986), this particular type of trichome and the presence of the distinctive conduplicate-spiral type of stigma provide the strongest morphological evidence for the common ancestry of the family. Benzing (1976, 1980) and Benzing et al. (1978) pointed out that the structural and physiological refinements of the foliar trichomes

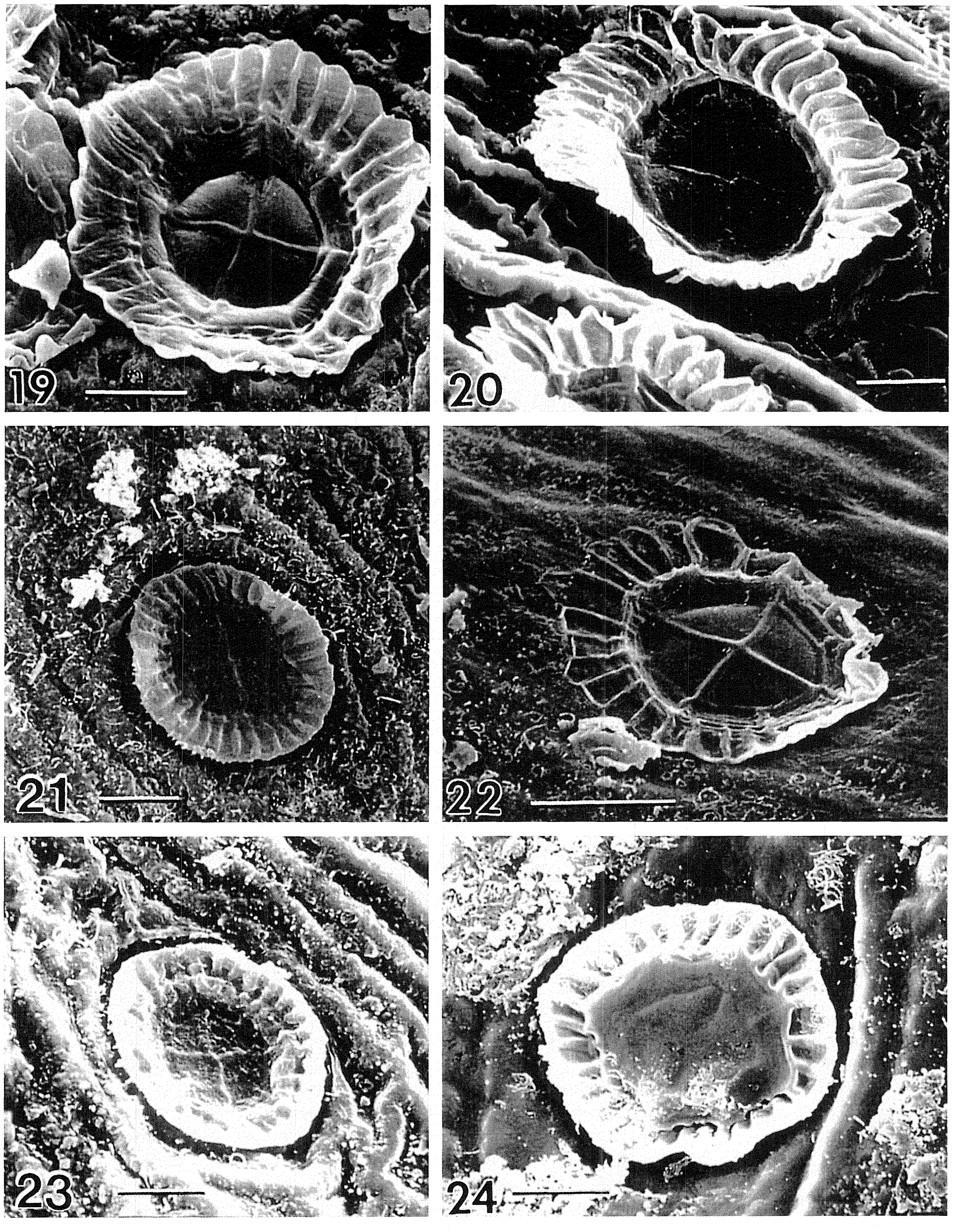

FIGURE 4. (Continued) **4.19.** *C. wangerinii* (Palací 1235), 4+8+34. **4.20.** *C. pisiformis* (Folsom 5038, MO), 4+8+40. **4.21.** *C. micrantha* (Hamilton & D'Arcy 608, MO), 4+8+32. **4.22.** *C. morreniana* (SEL 1981-0230), 4+8+26. **4.23.** *C. hahnii* (Palací 1234), 4+8+32. **4.24.** *C. berteroniana* (DBG 6772197), 4+8+32.

have favored the extensive habitat-preference diversification in the family, and especially the colonization of arid, nutrient-deficient, epiphytic habitats.

The Tillandsioideae-type of peltate trichome is composed of two parts, the stalk and the cap. The stalk consists of two basal cells, a variable number of stalk cells, and a dome cell. The stalk is wholly immersed in the epidermis and its cells are living at maturity. The cap is a lateral expansion of cells originating from the dome cell that is one cell layer thick and appressed against the epidermis. At maturity the cap will consist of two or three concentric series of cells, including a central disk, one or two series of ring cells, and an outermost ring of wing cells (FIGURE 4). The cap cells may exhibit unevenly thickened cell walls and are usually dead at maturity.

The organization of the cells in the trichome cap is variable among taxa. In Bromelioideae and Pitcairnioideae, the cap has an irregular or slightly radial arrangement of cells, without a clear distinction between ring cells and wing cells; even the differentiation of the central disk may be lacking in some species of *Deuterocohnia* Mez (Pitcairnioideae; Varadarajan & Gilmartin 1987). Most variation in the organization of the cap cells is interpreted as a derivation from a primitive 4+8+32 basic pattern (i.e., 4 central cells, 8 ring cells, and 32 wing cells; Tietze 1906, Tomlinson 1969). Strehl and Winkler (1981) proposed that certain phyletic relationships can be traced among the three subfamilies based on morphological characters of the foliar scales. They concluded that a trend can be traced from Pitcairnioideae to Bromelioideae to Tillandsioideae with increasing regularity, progressive fixation of the cell number, and a tendency for central cell increase from one to four. As Varadarajan and Gilmartin (1987) point out, however, more extensive developmental studies (e.g., Roguenant et al. 2001) are needed to determine structural homologies between different types of peltate trichomes.

Taxonomically, variation of leaf trichomes has shown some utility at the generic level (Tomlinson 1969). At the species level, however, variation in foliar scales has been of limited use (see Gardner 1983, Palací & Brown 1994, Beaman & Judd 1996, Roguenant et al. 2001), due in part to the high variability observed within species, and even between scales of different parts of the same leaf. Species of *Catopsis* typically exhibit a 4+8+32 cell pattern (4 central cells + one series of ring cells + one series of wing cells) in their cap (FIGURES 4.4, 4.6, 4.9). Tietze (1906) mentioned the presence of two concentric series of ring cells (i.e., 4+8+32+64) in the caps of *C. nitida, C. morreniana,* and *C. nutans,* but this pattern has not been confirmed in this study. The number of wing cells ranges from 20–26 in *C. morreniana* and *C. delicatula* L.B.Sm. (FIGURES 4.11, 4.22, 4.18) to 40–64 in *C. minimiflora* Matuda, *C. paniculata* s.s. and *C. pisiformis* (FIGURES 4.10, 4.1, and 4.20 respectively). Tomlinson (1969) observed that in *C. floribunda* the number of wing cells varied from 33 to 40 in scales from different parts of the same leaf. He attributed this variability to irregularities in the number of radial divisions in the outermost layer of wing cells. Similarly, Beaman and Judd (1996) reported "32 or 64" wing cells in the scales of four species of *Tillandsia,* depending on their location on the plant. In addition, Tomlinson (1969) observed that occasionally aborted or incompletely developed scales can be present towards the leaf base. Thus, the number of cells in leaf scales seems to be variable within a single plant, and species specific correlations should be considered with caution.

Additional variation was observed in the thickening of the adjacent anticlinal walls of wing cells. For example, the wing cells of *Catopsis floribunda* (FIGURE 2.9) and *C. juncifolia* exhibit distinctly uneven thickening, while those of *C. nutans* are evenly thin (FIGURE 2.10). There may be a correlation between the semimesic habit and uneven thickening in the anticlinal walls of wing cells.

Presence and density of trichomes themselves have been associated with habitat selection as well. Benzing and Renfrow (1971) found that leaves of the mesic, sparsely trichomed *Catopsis nutans* reflected significantly less visible light (21–30% reflectance) than the densely trichomed leaves of xerophytic *Tillandsia fasciculata* Sw. (42–47% reflectance). Similarly, Pierce et al. (2001) and Pierce (2003) found that reflectance was not significant for most bromeliad species, with the exception of atmospheric Tillandsias. The latter, by virtue of their highly ornate trichomes, were able to reflect up to 40% of light, providing significant photoprotection. In addition, the relative density and distribution of foliar scales and stomata have been correlated with habitat preference (Benzing et al. 1978). Tomlinson (1969) observed that the ratio of stomata to leaf scales decreases from less specialized terrestrial taxa to more specialized epiphytic species. Benzing (1976) also noted that trichome density is greatest in atmospheric epiphytes and lowest in mesic tank epiphytes. Benzing and Renfrow (1971) demonstrated that the layer of overlapping foliar scales in atmospheric species of *Tillandsia* greatly reduces CO_2 exchange when wet, and suggested that this phenomenon may be responsible for the exclu-

TABLE 1. Scale and stomata densities for abaxial leaf surfaces of representative species of *Catopsis* and some comparative values in the Tillandsioideae.

Species	Scales/mm^2 (SE)	Stomata/mm^2 (SE)	Stomata:scales (SE)	Reference
Catopsis sessiliflora	2.9 (0.7)	22.5 (1.8)	8.5 (1.9)	Palací 1997
C. montana	6.5 (1.0)	20.9 (1.8)	3.2 (0.5)	Palací 1997
C. berteroniana	8.0			Benzing & Renfrow 1971
C. floribunda	8.0			Benzing & Renfrow 1971
C. morreniana	8.5 (0.8)	23.0 (1.9)	2.8 (0.4)	Palací 1997
C. paniculata sp. 1 s.l.	10.8 (1.4)	20.7 (1.9)	2.0 (0.2)	Palací 1997
C. paniculata sp. 2 s.l.	13.8 (2.0)	18.6 (0.8)	1.4 (0.2)	Palací 1997
C. nutans	14.1			Benzing & Renfrow 1971
C. sessiliflora	15.3 (1.3)	19.8 (1.5)	1.4 (0.2)	Palací 1997
C. nutans	15.3 (1.3)	20.2 (2.8)	1.3 (0.2)	Palací 1997
C. nitida	15.3 (1.2)	31.7 (4.2)	2.1 (0.4)	Palací 1997
C. floribunda	16.4 (0.8)	33.1 (2.5)	2.0 (0.2)	Palací 1997
C. berteroniana	18.7			Benzing & Burt 1970*
C. juncifolia	19.9 (1.6)	34.8 (3.0)	1.8 (0.1)	Palací 1997
Average for *Catopsis*	12.4 (1.2)	24.5 (2.2)	2.6 (0.4)	
Mesic Tillandsioideae	23.3			Benzing 1976*
			2.4	Tomlinson 1969
Xeric Tillandsioideae	99.6			Benzing 1976*
			0.5	Tomlinson 1969
All Tillandsioideae	1.5			Tomlinson 1969
Avg. for xeric *Tillandsia*	54.9 (2.2)	15.0 (2.9)	0.3 (0.1)	Various (Palací 1997)

* Corrected to 1 mm^2.

sion of these species from wet and shaded environments. In *Catopsis* the average ratio of stomata to peltate trichomes is relatively high compared to xerophytic tillandsioids, and a trend of increasing foliar scale density from mesic to semi-mesic is apparent in the genus (TABLE 1, FIGURES 2.11–2.13). The ecophysiological significance of variation in foliar trichome and stoma densities in species with sparse, non-overlapping scales remains unknown (see Benzing 1976 for further discussion).

Despite the apparent homogeneity of morphological features in *Catopsis* species, variations in leaf shape and size and rosette type are of practical taxonomic importance, though quantitative variation and habitat/ecological variability within and between species needs to be considered. The anatomical features are relatively homogeneous, and have relevant ecological and ecophysiological importance, although little, if any, obvious taxonomic significance. Similarly, variation in leaf peltate trichome structure and distribution appears to be more associated with habitat preference and developmental variability within the leaf than with taxonomic circumscription. Additional research from an ecophysiological perspective is needed in order to understand the significance of several anatomical features of *Catopsis*. In particular, the role of epicuticular waxes, sparse trichome cover, and the variable development and physiological significance of water storage tissue need to be addressed.

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