American Journal of Botany 88(8): 1371–1389. 2001.

HYDROPHOBIC TRICHOME LAYERS AND EPICUTICULAR WAX POWDERS IN BROMELIACEAE[1]

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The distinctive foliar trichome of Bromeliaceae has promoted the evolution of an epiphytic habit in certain taxa by allowing the shoot to assume a significant role in the uptake of water and mineral nutrients. Despite the profound ecophysiological and taxonomic importance of this epidermal structure, the functions of nonabsorbent trichomes in remaining Bromeliaceae are not fully understood. The hypothesis that light reflection from these trichome layers provides photoprotection was not supported by spectroradiometry and fluorimetry in the present study; the mean reflectance of visible light from trichome layers did not exceed 6.4% on the adaxial surfaces of species representing a range of ecophysiological types nor was significant photoprotection provided by their presence. Several reports suggesting water repellency in some terrestrial Bromeliaceae were investigated. Scanning electron microscopy (SEM) and a new technique—fluorographic dimensional imaging (FDI)—were used to assess the interaction between aqueous droplets and the leaf surfaces of 86 species from 25 genera. In the majority of cases a dense layer of overlapping, stellate or peltate trichomes held water off the leaf epidermis proper. In the case of hydrophobic tank-forming tillandsioideae, a powdery epicuticular wax layer provided water repellency. The irregular architecture of these indumenta resulted in relatively little contact with water droplets. Most mesic terrestrial Pitcairnioideae examined either possessed glabrous leaf blades or hydrophobic layers of confluent trichomes on the abaxial surface. Thus, the present study indicates that an important ancestral function of the foliar trichome in Bromeliaceae was water repellency. The ecophysiological consequences of hydrophobia are discussed.

Key words: Bromeliaceae; epicuticular wax; fluorographic dimensional imaging; SEM; trichomes; water repellency.

Bromeliaceae are flowering plants that are popular in horticulture and also of great ecological importance in the Neotropics, occupying a diverse range of habitats. One of the first attempts to classify bromeliad diversity in an ecological context was made by Pittendrigh (1948), who elaborated on the observation of Tietze (1906) that life form and the function of leaf hairs was reflected in the taxonomic relationships of genera. Pittendrigh's scheme was further expanded by Benzing (2000) into the five ecophysiological types summarized in Table 1.

Leaf hairs or foliar trichomes (i.e., unicellular or multicellular structures arising from the epidermal tissues; Bell, 1991) are almost ubiquitous in Bromeliaceae (Benzing, 1976) and are perhaps the most distinguishing vegetative feature of the family. It is well documented that the peltate trichomes belonging to species with Type 3, 4, and 5 life forms support epiphytism by endowing the shoot with the capacity to augment or replace the absorptive functions of roots (Schimper, 1888; Billings, 1904; Mez, 1904; Benzing, 1970, 1976; Benzing and Burt, 1970; Benzing et al., 1976; Nyman et al., 1987; Smith, 1989; see Benzing [1980] for a detailed discussion of their mode of action). The trichomes of terrestrial Type 1 and many Type 2 bromeliads are incapable of this function (Benzing et al., 1976; Lüttge et al., 1986). Trichome function has therefore played a pivotal role in the adaptive radiation of Bromeliaceae via the operation of these different ecophysiological strategies.

However, the function(s) of the trichomes of Type 1 bromeliads remains enigmatic. Molecular phylogenetics indicates that the genera *Ayensua* and *Brocchinia* are basal to the rest of the family (Terry, Brown, and Olmstead, 1997; Horres et al., 2000; Crayn, Winter, and Smith, unpublished data). Although direct fossil evidence is negligible, mesic Type 1 Pitcairnioideae (e.g., *Ayensua*, some *Brocchinia, Fosterella, Pitcairnia*) are also considered to exhibit a primitive life form (i.e., ecophysiologically they most closely resemble a hypothetical ancestor of the family). This assessment is based not only on subfamilial characteristics such as the extensive root system (Tietze, 1906), but also on the presence of less advanced nonsucculent C_3 physiology (see Medina, 1974) and the simpler structure of the trichome (Benzing, 1980). Indeed, within the genus *Brocchinia* advanced Type 4 species possess absorbing trichomes, while nonimpounding terrestrial species possess less highly organized trichomes and are more basal within the genus (N.B. the most primitive of these, *B. prismatica*, possesses stellate trichomes similar to those of *Fosterella* species; Givnish et al., 1997). Thus, foliar trichomes of mesic Type 1 Pitcairnioideae mediate primitive functions.

Many roles other than water and nutrient absorption have been ascribed to bromeliad trichomes, but these functions often only apply to a small number of species (such as the attraction of pollinators or seed dispersers in the case of some *Tillandsia* and *Billbergia* species; Benzing, 2000). More general hypotheses concerning the function of bromeliad trichomes include obstruction of predators and pathogens (Benzing, 2000), reduction of transpiration (Billings, 1904), and photoprotection (Benzing and Renfrow, 1971; Lüttge et al.,

[1] Manuscript received 27 June 2000; revision accepted 1 February 2001.

The authors thank Harry E. Luther and Bruce K. Holst for assistance with identification, for generously putting the living collections and herbarium of the Marie Selby Botanic Gardens at our disposal, and, along with Darren M. Crayn, for providing comments on an early version of the manuscript; David H. Benzing for invaluable criticism during the review process; Jason R. Grant for aid with systematic issues; Jorge E. Aranda for collecting in Fortuna, Panama; Jorge Ceballos for invaluable technical support with the scanning electron microscope; and Richard Gottsberger and Aurelio Virgo for general assistance. We gratefully acknowledge support by a grant from the Andrew W. Mellon Foundation through the Smithsonian Tropical Research Institute.

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TABLE 1. Life forms or ecophysiological types of Bromeliaceae (after Benzing, 2000).

Life form	Characteristics
1	Terrestrial herbs of subfamily Pitcairnioideae (and many Bromelioideae) that use roots to acquire water and nutrients—the leaf hairs being nonabsorbent.
2	Terrestrial Bromelioideae with leaf bases that form a rudimentary watertight ''tank'' into which some axillary roots may grow.
3	Terrestrial or epiphytic herbs in subfamily Bromelioideae, the roots of which have reduced importance in water and nutrient acquisition with the leaf bases forming an extensive water-holding tank—predominantly crassulacean acid metabolism (CAM), with leaf hairs that have some capacity to take up water and nutrients.
4	Tank-forming epiphytes in subfamily Tillandsioideae and some *Brocchinia*—predominantly C_3 and with high densities of leaf hairs on the leaf bases that are highly effective at water and nutrient uptake, the roots functioning primarily as holdfasts.
5	Succulent CAM Tillandsioideae that are epiphytic or lithophytic, with leaf hairs taking up water directly over the entire leaf surface (without a tank) and possessing holdfast roots, if any.

1986). The deterrence of predators and pathogens currently has no experimental support. Reduction of transpiration is a xeromorphic adaptation, and as such, it is unlikely that this would be an important selection pressure acting on ancestors in mesic habitats.

In high densities, bromeliad trichomes produce a whitish leaf surface that reflects light when dry. This has been quantified in Type 4 *Tillandsia fasciculata* (Benzing and Renfrow, 1971) and semimesic Type 1 *Pitcairnia integrifolia* (Lüttge et al., 1986) and is highly suggestive of a role in photoprotection. However, in the more relevant case of Type 1 *P. integrifolia,* trichomes are restricted to the abaxial surface of the leaf; had these trichomes developed primarily to serve a photoprotective role, then they would be expected to occur at least in equal densities on the glabrous adaxial surface. Lüttge et al. (1986) note that the edges of the leaves of *P. integrifolia* roll inwards to expose the trichomed abaxial surface during the dry season, perhaps to promote reflectance, and propose this as a form of regulation of light reflectance. However, this behavior may occur simply as a consequence of drought in glabrous species (e.g., *Pitcairnia valerii*; personal observation), perhaps as a response to water loss and concomitant shrinkage of water-storage parenchyma in the hypodermis (see Billings, 1904). More importantly, the trichomes of *P. integrifolia* and *P. bifrons* were not found to influence the heating of leaves (Lüttge et al., 1986). Thus, a photoprotective role for trichomes remains without direct supporting evidence; an investigation of photoinhibition using fluorimetry techniques has yet to be undertaken.

Evidence for a further general hypothesis concerning the role of the trichome in terrestrial Bromeliaceae is present in the literature, but has apparently been overlooked. Krauss (1948–1949) working on *Ananas comosus* noted that ''the trichomes on the lower surface of the leaf blade proper appear unwettable. Drops of water placed on this surface do not spread, but remain unabsorbed for experimental periods of 3 to 6 h.''

Krauss (1948–1949) also went on to observe that, whereas the absorbent trichomes of *Tillandsia usneoides* lost their pale whitish color when wetted (Billings, 1904), those on the abaxial surface of *A. comosus* did not, as a consequence of air trapped beneath the trichomes. This implies that the trichomes on the abaxial surface of *A. comosus* repel water. Also, the abaxial surfaces of *Pitcairnia integrifolia* and *P. macrochlamys* leaf blades appear to be unwettable (Benzing, Seemann, and Renfrow, 1978; Lüttge et al., 1986), and in the case of *P. integrifolia,* ''water repellent.'' Indeed, Benzing (1970) discovered that after 12 h of exposure the abaxial surface of *P. macrochlamys* had absorbed ~3.5 times less $zinc^{65}$ than the glabrous cuticle of the adaxial surface, perhaps suggesting that the trichome layer hindered absorption. Widespread occurrence of repellent trichome layers on the abaxial leaf blade surfaces of mesic Type 1 bromeliads would therefore suggest that hydrophobia was an important property of the foliar trichome in ancestral Bromeliaceae.

Also relevant to this study are the hydrophobic waxy surfaces of *Brocchinia reducta* and *Catopsis berteroniana.* Tomlinson (1969) suggests that in the case of *C. berteroniana* these promote the run-off of water from the leaf blades into the tank and attraction and entrapment of insect prey by these carnivorous species have also been suggested (Fish, 1976; Frank and O'Meara, 1984). These species also share advanced Type 4 life forms, which usually possess hydrophilic trichomes at least lining the tank. Determinations of the occurrence of hydrophobic surfaces in Tillandsioideae and *Brocchinia* could shed additional light on the evolution of the Type 4 life form.

The present study employs a novel technique, fluorographic dimensional imaging (FDI), to assess the interactions between aqueous droplets and the leaf blade surfaces of 86 ecologically diverse bromeliad species representing 25 genera and all three subfamilies. Fluorographic dimensional imaging is used in conjunction with scanning electron microscopy (SEM) and spectroradiometry to reveal the mechanism by which certain trichomes and epicuticular wax powders repel water. Fluorimetry is used to investigate the hypothesized role of trichomes and wax layers in photoprotection. Nomenclature follows that of Luther and Sieff (1998), with the exception of the recently rejected genus *Pepinia* (Taylor and Robinson, 1999), which is recognized as a subgenus of *Pitcairnia* (sensu Smith and Downs, 1974).

MATERIALS AND METHODS

Plant material of Panamanian origin was collected from the wild, with voucher specimens being held at the main herbarium of the Smithsonian Tropical Research Institute, Panama (herbarium code SCZ) and at the University of Panama (PMA). Material of Trinidadian origin was obtained from the living collections of Moorbank Botanic Gardens (Newcastle-upon-Tyne, UK). *Ananas comosus* was grown from meristem culture, with original material provided by the Centre International de Recherche en Agronomie et Development (Montpellier, France). All other material was obtained from the living collections at the Marie Selby Botanic Gardens, Sarasota, Florida, USA (accession numbers available on request).

Repellency was denoted by the depth of aqueous droplets on adaxial and abaxial leaf blade surfaces. For FDI of aqueous droplets, calibration standards were prepared using glass coverslips (~2 cm wide), one-half being coated with a flat film of paraplast wax (Sigma Chemical, St. Louis, Missouri, USA), and the other half remaining as an exposed glass surface. The thickness of these wax and glass standards was measured by micrometer, and these standards were lightly fixed along one edge of a strong glass plate of ~40 × 40 cm.

Leaf discs were cut from intact and surface denuded midleaf portions of leaf blade (from two-thirds of the way along the blade). In many species denudation was achieved using sticky tape, although some species such as *Ananas comosus* required careful scraping with a scalpel blade. In the case of apparently glabrous leaves, the procedure of denudation with sticky tape was conducted for the sake of consistency. Leaf discs from replicate leaves (where possible from separate individuals) were then fixed in rows onto the glass plate, with intact and denuded examples of both surfaces presented uppermost.

Droplets (10-μL each) of 0.05% (mass by volume in distilled H_2O) fluorescein sodium solution were quickly pipetted onto the surface of the leaf discs and calibration standards and left to stand for 40 min in a darkened room. In these darkened conditions, the leaf discs and standards were then illuminated with an ultraviolet (UV) transilluminator (Fotodyne, Hartland, Wisconsin, USA), and the resulting fluorescence from the excited fluorochrome was photographed using a level camera mounted directly above the leaf discs. Initial tests determined that the following camera settings provided the greatest depth of field and contrast, with well-exposed fluorescence and a darkened background: an aperture of f/22, aperture priority (or a 9-sec exposure with a cable release), using ISO 100/DIN 21° color-reversal film (Kodak Elite). The depth of droplets on wax and glass standards was determined by micrometer immediately after the fluorograph was taken.

After processing, fluorographs were digitally scanned (LS-2000, Nikon, Shinagawa-Ku, Tokyo, Japan) and the luminosity of fluorescein droplets was determined using Corel PHOTO-PAINT7 (Corel, Ottawa, Ontario, Canada) imaging software (selecting each particular region of the image with the "eyedropper" tool, and recording the luminosity (L) of the "paint" color). To compensate for possible uneven lighting, eight measurements were taken from each droplet, and the measurements were averaged. Luminosity and depth data from the glass and wax standards were then regressed (Excel, Microsoft, Seattle, Washington, USA) to create a calibration equation, from which the depth of droplets on leaf discs was calculated using respective luminosity values. This technique allowed rapid, inexpensive, mass screening of samples. The difference in droplet depth (ΔD) due to surface features can be summarized by the following equation:

$$\Delta D_{\mathrm{d\ (b)}} = i_{\mathrm{d\ (b)}} - e_{\mathrm{d\ (b)}} \quad (1)$$

where i = droplet depth on intact surface, e = droplet depth on denuded surface, d = adaxial surface or alternatively b = abaxial surface.

In order to examine the effect of water surface tension on the interaction between trichomes and water, the above FDI technique was also used on the leaves of *Ananas comosus,* using droplets (10-μL each) of fluorescein sodium solution (5 mL of 0.05% fluorescein and 0.5 mL distilled H_2O); with further replicates on which 10-μL droplets of a solution of fluorescein and household detergent (5 mL of 0.05% fluorescein and 0.5 mL neat detergent) were used.

Reflectance of light by leaves was measured using an LI-1800 portable spectroradiometer (LI-COR, Lincoln, Nebraska, USA), via an 1800–12s external integrating sphere (LI-COR). Ranges of reflectance values were normalized to 100% using barium sulfate ($BaSO_4$) as a standard; this compound has an absolute reflectivity of 99.3% in the wavelength range 300–800 nm (Munsell Color, New Windsor, New York, USA). Measurements were taken of intact, water-inundated, and denuded leaf surfaces (both adaxial and abaxial). Species with water repellent trichome layers were inundated by soaking in water for 1 h or until a surface film of water could be sustained on their removal from the water. Once again, in the case of surfaces that appeared to have no trichomes, the denudation process was carried out with sticky tape for consistency's sake. Average reflectance values of photosynthetically active radiation (PAR) were calculated as a mean across the wavelength range 400–700 nm. The reflectance conferred by trichomes or wax powders is defined as the difference in mean reflection between intact and denuded surfaces.

Photoinhibition of photosystem II was investigated using a PAM-2000 portable modulated fluorimeter (H. Walz, Effeltrich, Germany). *Aechmea dactylina, Ananas comosus* cv. Cayenne Lisse, *Catopsis micrantha, Pitcairnia integrifolia, Tillandsia flexuosa,* and *Werauhia sanguinolenta* were maintained in seminatural conditions in an open-sided greenhouse at the main Smithsonian Tropical Research Institute facility in Panama. Excluding the cultivar of *Ananas comosus,* these species grow in semi-exposed to exposed microhabitats and may experience several hours of direct sunlight each day (Lüttge et al., 1986; personal observations). A treatment of excessive excitation therefore consisted of transferring plants grown in moderate sunlight (~450 μmol photon·m^{-2}·sec^{-1} at midday) to direct sunlight at midday (PPFD ≈1700 μmol photon·m^{-2}·sec^{-1}) for 1 h. The degree of photoinhibition was denoted by the decline in the dark-adapted ratio of variable to maximum chlorophyll fluorescence (F_v/F_m) following this treatment, with intact and denuded surfaces being compared.

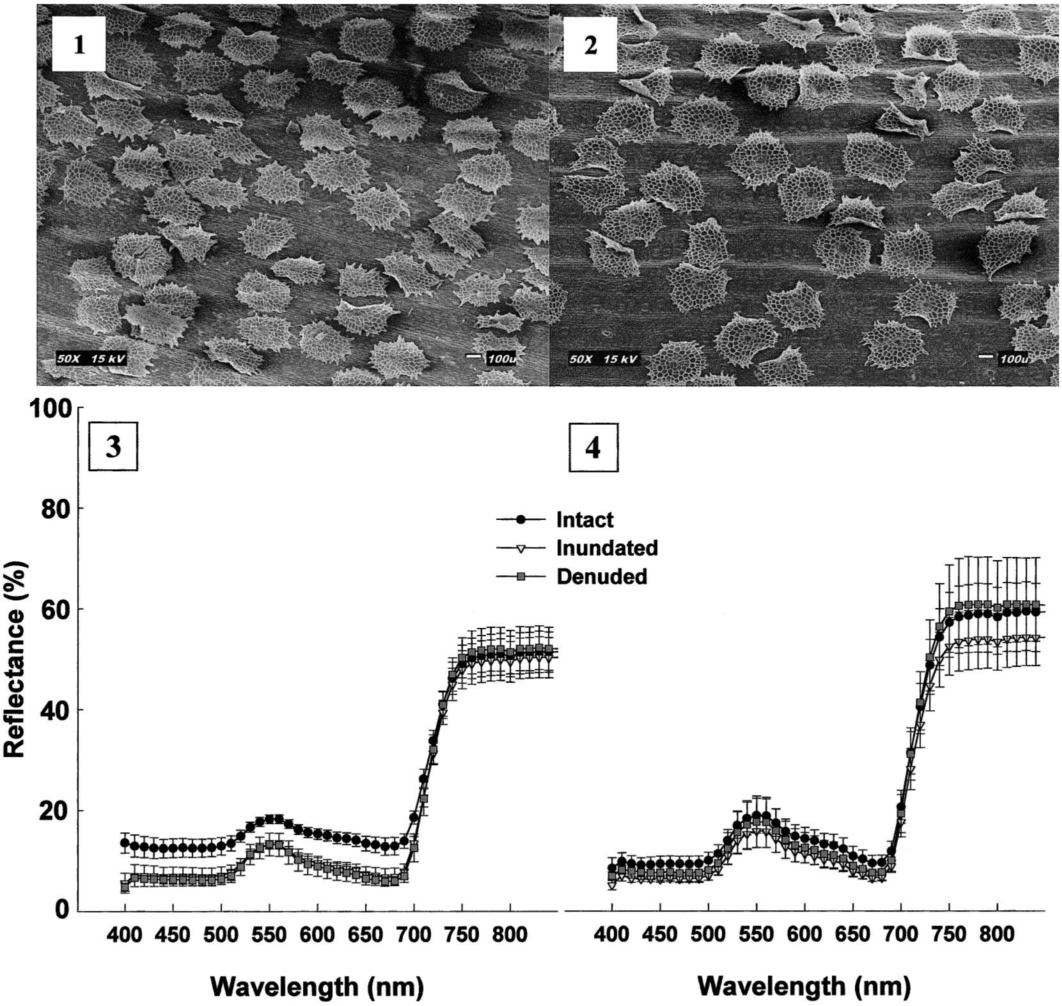
For scanning electron microscopy, the majority of leaf samples were dehydrated through an alcohol series, critical point dried (CPD) in CO_2, and then sputter-coated with gold-palladium (Hummer VI-A, Anatech, Springfield, Virginia, USA) before examination in the scanning electron microscope (Jeol JSM-5300LV, Jeol, Tokyo, Japan). However, samples of *Catopsis* were not dehydrated in this manner, as the solvents used in CPD may destroy the structure of wax surfaces (Juniper and Jeffree, 1983); samples were placed in the scanning electron microscope without preparation.

RESULTS

Light reflectance and photoprotection—An intact layer of dry trichomes increased the reflectance of visible light (400–700 nm) by an average of 6.4% on the adaxial surface of *Aechmea dactylina,* although not significantly on the abaxial surface ($P > 0.05$; Figs. 1–4). Reflectance was increased by 5.0 and 3.9% on adaxial and abaxial surfaces, respectively, of *Tillandsia flexuosa* (data not shown), 4.9 and 10.6% on adaxial and abaxial surfaces of *Ananas comosus* (Figs. 5–8), and 17.8% on the abaxial surface of *Pitcairnia integrifolia* (but not on the glabrous adaxial surface; Figs. 9–12). Powdery epicuticular wax increased reflectance of visible light by a mean of 6.3 and 6.6% on adaxial and abaxial surfaces, respectively, of *Catopsis micrantha* (Figs. 13–16). Low densities of filmy trichomes were observed via SEM on the adaxial surface of Type 4 *Werauhia sanguinolenta,* but these did not alter reflectance (data not shown). The increased reflectance conferred by trichomes or wax was not sufficient for photoprotection, with the extent of photodamage (as denoted by a percentage decline in F_v/F_m) exhibited by leaves with intact surfaces equaling that of leaves denuded of trichomes or wax powders (after exposure to an equivalent and excessive photon dose; Table 2).

When inundated with water, the adaxial surfaces of *Aechmea dactylina* and *Ananas comosus* (Figs. 3, 7) and both surfaces of *Tillandsia flexuosa* lost the reflectivity conferred by their trichomes. The trichomes of *Pitcairnia integrifolia* and those of the abaxial surface of *Ananas comosus* retained their reflectivity when treated in this manner (Figs. 8, 12). A surface film of water could not be sustained on the leaves of *Catopsis micrantha* even after several days of inundation. Indumenta did not increase the reflectance of infrared light (800 nm) in most species, except for *Catopsis micrantha* and *Pitcairnia integrifolia.* Reflectance of infrared wavelengths was higher (40–50%) than the reflectance of visible light in all species studied.

Leaf blade interactions with water—A typical fluorograph for a single species (*Catopsis micrantha*) is shown in Fig. 17. Fluorographic dimensional imaging determined that droplet depth had diminished after 40 min on the intact leaf blade surfaces of Type 5 species when compared with surfaces denuded of trichomes (ΔD). For example, on leaf blades of *Til-*



Figs. 1–4. *Aechmea dactylina* leaf blade surfaces. **1–2.** Scanning electron micrographs of the adaxial and abaxial surfaces, respectively. **3–4.** Reflectance of light by the adaxial and abaxial surfaces, respectively. Reflectance data represent the mean ± 1 SE of four replicates.

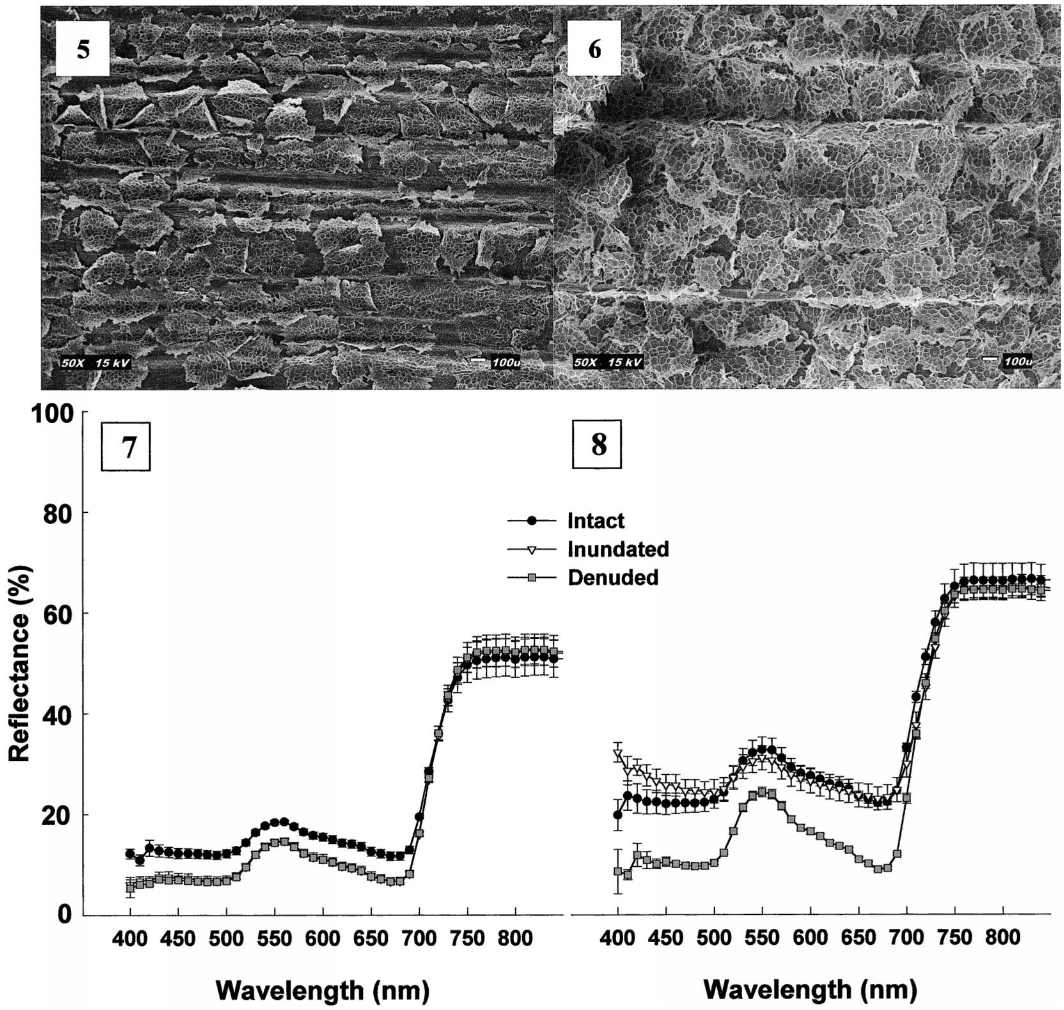
landsia nana, $\Delta D_d = -732$ and $\Delta D_b = -876$ μm; confirming these leaves to be highly hydrophilic.

Droplets exhibited no significant difference in depth between intact and denuded leaf blade surfaces in most Type 4 species ($P \leq 0.05$; Table 3). However, there were some notable exceptions; for example the hydrophobic abaxial surface of *Vriesea monstrum* ($\Delta D_d = 214$ μm; Table 3) and both hydrophilic surfaces of *Tillandsia elongata* ($\Delta D_d = -210$ μm and $\Delta D_b = -190$ μm). Many Type 4 taxa possessed hydrophobic waxy surfaces, e.g., *Catopsis micrantha* ($\Delta D_d = 800$ μm and $\Delta D_b = 960$ μm), *Guzmania macropoda* ($\Delta D_b = 216$ μm), and *Werauhia capitata* ($\Delta D_b = 350$ μm).

Trichomes, but not wax, lent subfamily Bromelioideae a range of interactions with leaf surface water. This included no interaction at all (e.g., both surfaces of Type 2 *Bromelia pinguin*; Table 3), hydrophilic surfaces (e.g., Type 3 *Aechmea dactylina*, $\Delta D_d = -220$ μm and $\Delta D_b = -130$ μm; Type 3 *A. fendleri*, $\Delta D_d = -130$ μm and $\Delta D_b = -110$ μm), and the hydrophobic abaxial surfaces of species such as Type 2 *Ananas comosus* ($\Delta D_b = 160$ μm; Fig. 8) and Type 1 *Ronnbergia explodens* ($\Delta D_b = 100$ μm). A number of bromelioid species possessed both hydrophilic adaxial surfaces and hydrophobic abaxial surfaces (e.g., Type 3 *Aechmea nudicaulis*, $\Delta D_d = -267$ μm and $\Delta D_b = 226$ μm; Type 1 *Cryptanthus whitmanii*, $\Delta D_d = -205$ μm and $\Delta D_b = 407$ μm; Type 1 *Orthophytum benzingii*, $\Delta D_d = -477$ μm and $\Delta D_b = 474$ μm).

Of the mesic Type 1 pitcairnioids, genera such as *Fosterella* and *Pitcairnia* either possessed hydrophobic abaxial surfaces, due solely to trichome cover (e.g., *Pitcairnia integrifolia*, $\Delta D_b = 230$ μm), or were entirely glabrous and noninteractive (e.g., *Pitcairnia patentiflora*), with a small number possessing hydrophobic adaxial surfaces (*Pitcairnia arcuata*, $\Delta D_d = 310$ μm). The more xeromorphic pitcairnioid genera showed a range of trichome-mediated interactions with surface water, including species that possessed both hydrophilic and hydrophobic leaf blade surfaces (e.g., *Dyckia marnier-lapostollei*, $\Delta D_d = -457$ μm and $\Delta D_b = 740$ μm; Table 3).

Of the 16 species examined from the elfin cloud forest at Cerro Jefe in central Panama, six possessed water-repellent leaf surfaces (Table 3). These were either Type 1 species with repellent trichomes (*Pitcairnia arcuata, Ronnbergia explodens*) or Type 4 species with relatively upright leaves that used trichomes (*Vriesea monstrum*) or epicuticular wax powders (*Catopsis micrantha, Guzmania macropoda, Werauhia capitata*) to shed water. A further six were Type 4 species equipped with hypostomatous and horizontally orientated leaves.



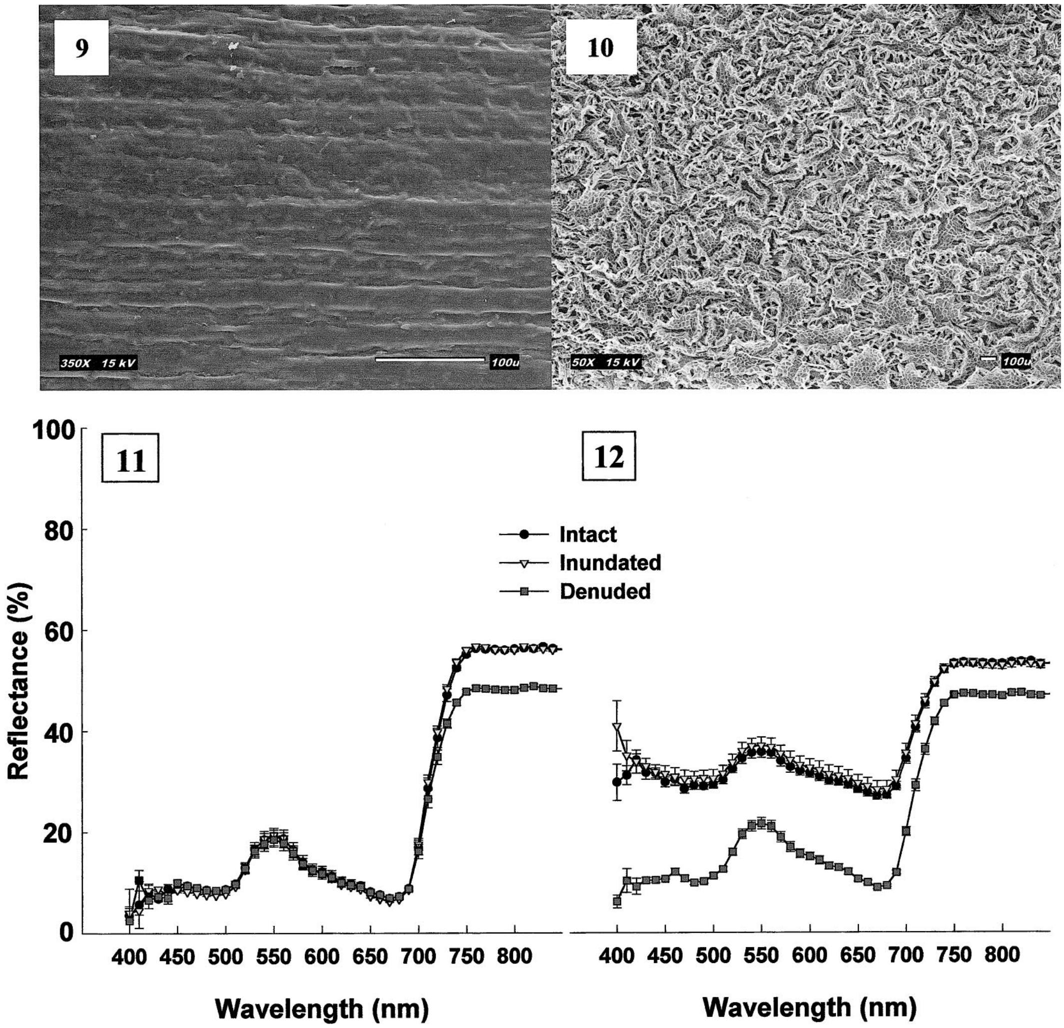
Figs. 5–8. *Ananas comosus* leaf blade surfaces. **5–6.** Scanning electron micrographs of the adaxial and abaxial surfaces, respectively. **7–8.** Reflectance of light by the adaxial and abaxial surfaces, respectively. Reflectance data represent the mean ± 1 SE of four replicates.

The wax powder layer of *Catopsis micrantha* was less pronounced towards the tip of the leaf blade, where it still promoted beading up of water (Figs. 18, 19). This layer was continuous over the leaf blade surface (Figs. 13, 15, 20), but was not present on the adaxial surface of the leaf sheath within the tank of the plant. This surface is densely covered with peltate trichomes (Fig. 21). Powdery epicuticular wax was also present on hydrophobic surfaces of *Alcantarea odorata, Brocchinia reducta,* and *Werauhia capitata* (Figs. 22–25).

Surfaces that showed no trichome- or wax-mediated interaction with water generally either possessed thin, filmy peltate trichomes (e.g., the adaxial surface of *Vriesea monstrum*; Fig. 26) or lacked surface structures (e.g., the adaxial surfaces of *Fosterella petiolata, Pitcairnia corallina, Pitcairnia integrifolia*; Figs. 9, 27, 28). Water repellent trichomed surfaces featured either high densities of large, overlapping peltate trichomes consisting mainly of extrusive ring cells (i.e., ''ring-peltate'' trichomes; Figs. 6, 10, 29–31) or low densities of tangled stellate trichomes forming a discontinuous indumentum (e.g., *Pitcairnia arcuata*; Fig. 32). Trichomes of *Puya laxa* did not significantly interact with water droplets ($P \leq 0.05$; Table 3)—this species possesses two types of trichome, one being highly modified with an elongate wing that spirals around itself to form a hair-like structure (Fig. 33).

Low densities of ring-peltate trichomes occurred on the hydrophilic surfaces of *Aechmea dactylina* (Figs. 1, 2, 34, 35). Individual trichomes were structurally comparable to the trichomes comprising the continuous hydrophobic trichome layers of *Ananas comosus, Fosterella petiolata, Pitcairnia corallina, Ronnbergia explodens,* and *Vriesea monstrum* (Figs. 6, 29–31, 36, 37). None of these species possessed wax powders, either on the trichomes or elsewhere.

On the hydrophilic adaxial surface and hydrophobic abaxial surface of *Cryptanthus whitmanii* the trichomes appeared no different, although the lower densities on the adaxial surface revealed the leaf epidermis proper to SEM (Figs. 38, 39). *Aechmea nudicaulis* also has low densities of thin, filmy trichomes on the hydrophilic adaxial surface (Fig. 40) and a typical hydrophobic abaxial surface (Fig. 41). No species in any subfamily possessed a hydrophobic adaxial surface combined with a hydrophilic abaxial surface. Water repellent epicuticular wax powders or confluent layers of large ring-peltate trichomes occurred exclusively on surfaces that possessed stomata in the species studied.



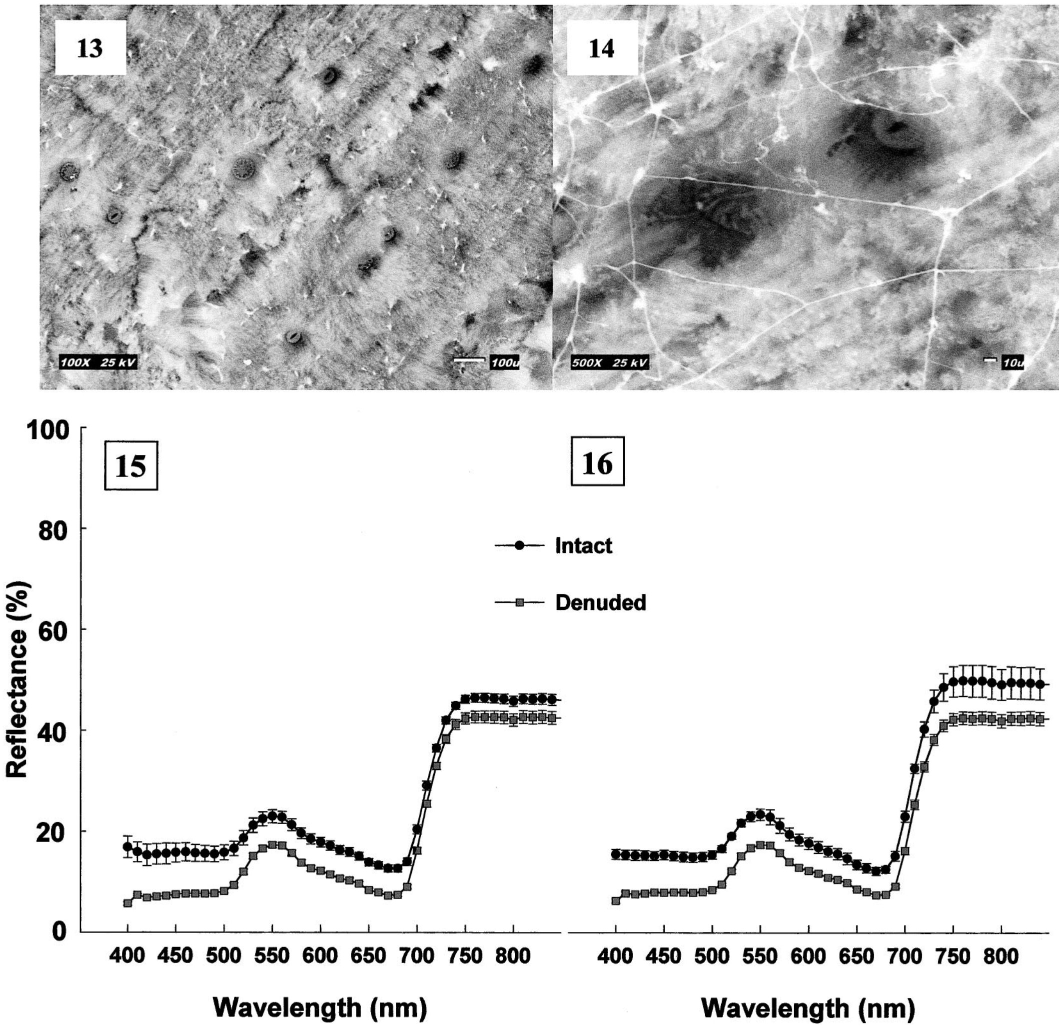
Figs. 9–12. *Pitcairnia integrifolia* leaf blade surfaces. **9–10.** Scanning electron micrographs of the adaxial and abaxial surfaces, respectively. **11–12.** Reflectance of light by the adaxial and abaxial surfaces, respectively. Reflectance data represent the mean ± 1 SE of four replicates.

The addition of detergent to the fluorescein solution used in FDI resulted in higher wettability of both adaxial and abaxial surfaces of *Ananas comosus*, with aqueous droplets (10-μL volume) spreading to negligible depth (14.8 ± 3.2 μm adaxially and 17.6 ± 5.3 μm abaxially; Table 4) when the surface tension of the water was reduced in this manner.

DISCUSSION

Light reflectance and photoprotection—The data indicate that trichomes and epicuticular wax powders do not have a significant photoprotective function in a range of ecophysiological types (Types 1–4). Trichomes either did not increase light reflectance from leaf blades (e.g., *Werauhia sanguinolenta*) or the mean reflectance conferred by trichomes or wax did not exceed 6.4% on the adaxial surfaces of the species studied (with up to 17.8% on the abaxial surfaces). This was not sufficient to significantly alter down-regulation of photosystem II by excess light in these species (Table 2). Indeed, trichomes and epicuticular wax powders conferring reflectances of between ~45 and 55% photoprotect certain desert plants (Ehleringer and Björkman, 1976; Robinson, Lovelock, and Osmond, 1993). Also, the present study indicated that the reflectance conferred was correlated with the mode of interaction between surfaces and water. Hydrophobic surfaces did not lose reflectivity when wet, whereas hydrophilic trichomes did (see also Billings, 1904; Krauss, 1948–1949; Benzing, Seemann, and Renfrow, 1978), and higher reflectivities on abaxial surfaces were correlated with the presence of dense hydrophobic indumenta (e.g., *Ananas comosus*, *Pitcairnia integrifolia*). Thus, the data indicate that hydrophobic and dry hydrophilic trichome layers inherently scatter light, but are unlikely to have evolved primarily for the purpose of photoprotection in Bromeliaceae.

The highly unusual, woolly trichomes of *Puya laxa* (Fig. 33) did not interact with water droplets on the leaf surface (Table 3). These trichomes probably act as protection against frost damage as exhibited by a number of *Puya* species growing in high altitude habitats (Miller, 1994). As this example illustrates, distinct taxa produce trichomes that represent a more specific adaptation to local environmental conditions. Thus, dense indumenta could yet prove to furnish photoprotection in the case of more extreme xerophytes (Type 5 species). A thorough investigation of the fluorescence characteristics of this life form was beyond the scope of the present study.



Figs. 13–16. *Catopsis micrantha* leaf blade surfaces. **13–14.** Scanning electron micrographs of the adaxial and abaxial surfaces, respectively. **15–16.** Reflectance of light by the adaxial and abaxial surfaces, respectively. Reflectance data represent the mean ± 1 SE of four replicates.

TABLE 2. Decrease in F_v/F_m (the dark-adapted ratio of variable to maximum chlorophyll fluorescence) of six species after exposure to saturating light (PPFD ≈1700 μmol·m^{-2}·s^{-1}) for 1 h, with the leaf blade surface either intact or denuded of surface features. Values are means ±1 SE of four replicates. The absence of differences in letters (a) between means of intact and denuded treatments indicates that there were no significant differences at the $P \leq 0.05$ level as determined by Student's *t* test. Life forms or ecophysiological types follow Benzing (2000).

Species	Life form	Surface	Decrease in F_v/F_m (%) Intact	Decrease in F_v/F_m (%) Denuded
Aechmea dactylina	3	Adaxial	30.0 ± 7.6 a	37.9 ± 8.8 a
		Abaxial	26.9 ± 5.8 a	30.1 ± 5.9 a
Ananas comosus	2	Adaxial	58.5 ± 5.6 a	43.8 ± 6.5 a
		Abaxial	26.3 ± 4.7 a	29.2 ± 3.4 a
Catopsis micrantha	4	Adaxial	29.4 ± 8.7 a	28.2 ± 3.2 a
		Abaxial	22.5 ± 5.0 a	29.5 ± 1.7 a
Pitcairnia integrifolia	1	Adaxial	52.7 ± 4.9 a	48.4 ± 2.7 a
		Abaxial	35.6 ± 6.3 a	39.0 ± 1.4 a
Tillandsia flexuosa	4–5	Adaxial	11.7 ± 4.1 a	21.1 ± 8.7 a
		Abaxial	30.7 ± 9.1 a	38.2 ± 10.1 a
Werauhia sanguinolenta	4	Adaxial	47.3 ± 7.2 a	39.4 ± 3.2 a
		Abaxial	34.1 ± 1.4 a	30.9 ± 2.7 a

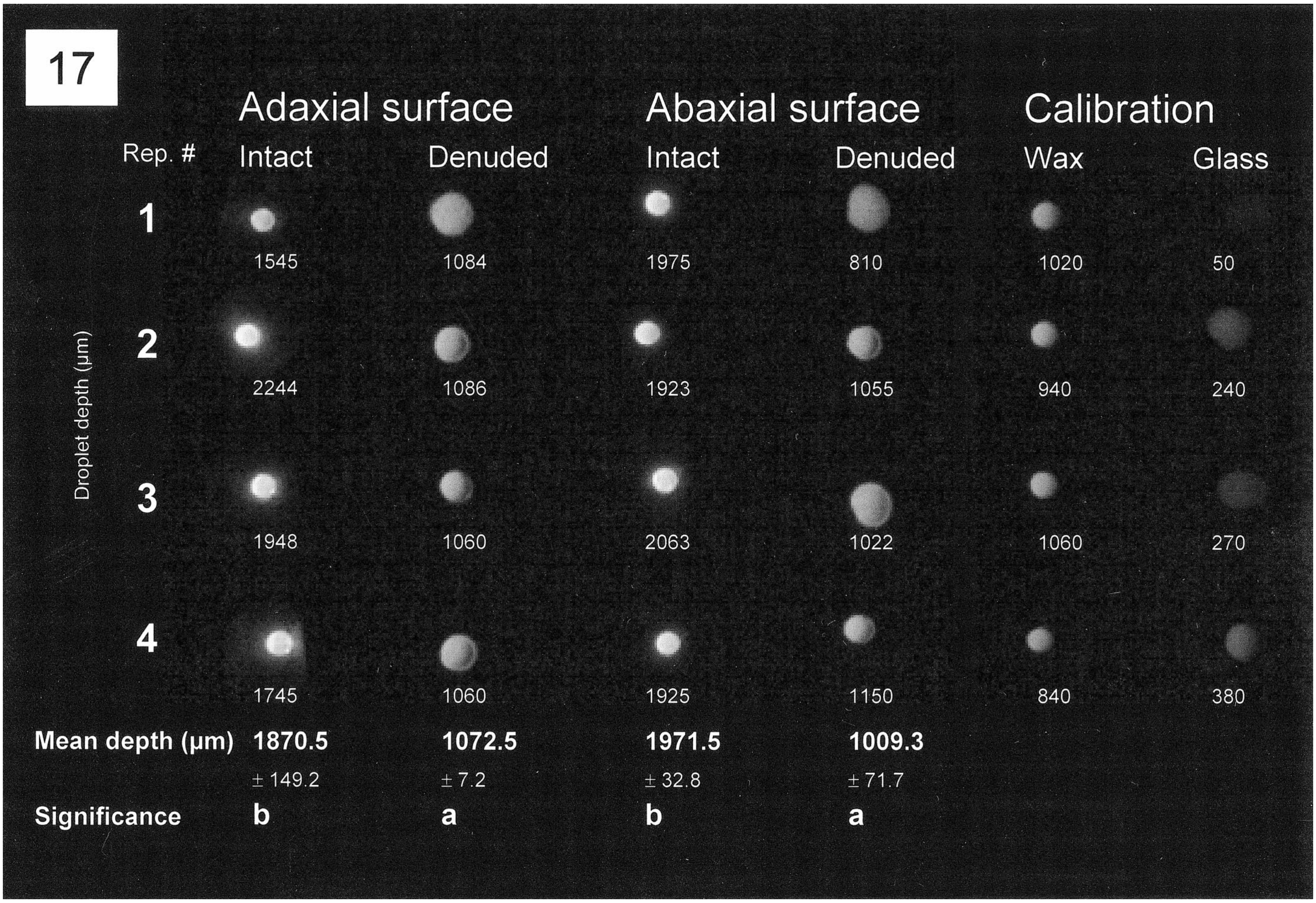


Fig. 17. A typical fluorograph for a single species (*Catopsis micrantha*), used to determine the depth of aqueous droplets on leaf disc surfaces (denoting repellency) via the comparison of fluorescence signatures of fluorescein droplets against calibration droplets of known depth. In this example, epicuticular wax powder layers from the adaxial and abaxial leaf blade surfaces are either present (intact) or removed (denuded). Mean depth values presented include ± 1 SE, with significant differences between means (at the $P \leq 0.05$ level) of four replicates determined using Fisher's multiple comparison procedure.

The mechanism of water repellency—Brewer, Smith, and Vogelmann (1991) noted three kinds of interaction between water and the trichomes of flowering plants: (1) low trichome densities that do not influence droplet retention or the location of surface moisture, (2) low densities of trichomes that induce surface water to aggregate into patches, and (3) high densities of trichomes that lift water off the leaf surface. The leaf blade surfaces of many Type 4 bromeliads exhibit low trichome densities (Benzing, 1980) and did not interact detectably with surface water in the present study (Table 3). Bromeliads that have low densities of attenuated stellate trichomes, such as Type 1 *Pitcairnia arcuata*, appear to interact with water as described by situation 2, loosely aggregating surface droplets. Consistent with the third, 'lifting,' mechanism of repellency, continuous layers of powdery wax or ring-peltate trichomes produce an irregular hydrophobic surface that prevents water from coming into contact with the epidermis proper. A summary of the principal interactions between leaf blade trichome layers and water within each ecophysiological type is presented in Table 5.

In many families of flowering plants, water droplets bead up more readily on irregular than uniform surfaces because the droplet only contacts the tips of projections from the cuticle (Holloway, 1968; Juniper and Jeffree, 1983), obviating adhesion (Brewer, Smith, and Vogelmann, 1991; Watanabe and Yamaguchi, 1993). The physics of these surface–water interactions are outlined by Barthlott and Neinhuis (1997). This hydrophobic mechanism is readily demonstrable in Bromeliaceae. For example, a wetted pineapple leaf (*Ananas comosus*) will lose the pale coloration of the abaxial surface only if detergent is first added to the water. Species with absorbent trichomes, on the other hand, lose this pale coloration and reflectivity immediately on wetting (Billings, 1904; Benzing and Renfrow, 1971; Benzing, 1980; Fig. 3). Also, droplets of water will only spread on the abaxial leaf surface of pineapple if detergent is added (demonstrated quantitatively in Table 4). Pineapple leaves soaked overnight in a detergent solution or 100% acetone will regain their repellency if subsequently rinsed and dried, suggesting a physical rather than chemical mechanism (personal observations). Additionally, if a pineapple leaf is partially dipped into a detergent solution rather than pure water, then liquid will be drawn or ''wicked'' up out of the solution along the trichome layer, i.e., once the surface tension of the water is broken the leaf surface becomes strongly hydrophilic. Thus, the physical properties of water are central to the mechanism of repellency. This mechanism also demonstrates, at least in part, how Type 4 species prevent water loss from the tank via capillary action.

Trichomes that characterize hydrophilic and hydrophobic surfaces usually share the same structure, with trichome density differing (e.g., the adaxial and abaxial surfaces of *Cryptanthus whitmanii* and hydrophilic *Aechmea dactylina* compared with hydrophobic *Ronnbergia explodens*; Figs. 34–39). The lower densities of peltate trichomes of *Aechmea dactylina* and the adaxial surface of *Cryptanthus whitmanii* would allow water to come into contact with the epidermis proper, with the interaction between the two presumably allowing water to spread and envelop trichomes. In addition, the adaxial trichomes of *Aechmea nudicaulis* differ structurally—lacking the irregular surface characteristic of the hydrophobic abaxial indumentum (Figs. 40, 41). The chemical composition of hydrophilic and hydrophobic surfaces in Bromeliaceae has not been investigated and the degree to which chemical vs. morphological interactions contribute to repellency remains undetermined. Nevertheless, the physical characteristics of hydrophobic trichome layers in Bromeliaceae are typical of water-repellent surfaces in other families, and the qualitative tests above suggest that surface morphology is paramount to the operation of hydrophobia.

Ecophysiological consequences of a hydrophobic indumentum—It may be significant that the majority of bromeliads are hypostomatous (Tomlinson, 1969; Benzing and Burt, 1970), with stomata and hydrophobic trichome layers occurring together. Intriguingly, Barthlott and Neinhuis (1997) demonstrate that particulate matter will adhere more readily to water droplets than to hydrophobic leaf surfaces, lending such leaves a ''self-cleaning'' capability when wetted. In concert with a possible function as a physical barrier to pathogens (Benzing, 2000), this self-cleaning effect could remove pathogens and prevent the physical blockage of stomata by particulates. A continuous trichome layer could also deter herbivores from the softer underside of the leaf, although to date this protective role is only evident in two species possessing glandular trichomes (see Benzing, 2000).

Benzing, Seemann, and Renfrow (1978) determined that photosynthetic gas exchange was not inhibited by wetting the leaf blades of six species on the surfaces of which water did not spread (including *Pitcairnia macrochlamys*). Conversely, the wetted trichomes of Type 5 bromeliads hold films of water that slow the exchange of gases between the air and the leaf (Benzing, Seemann, and Renfrow, 1978; Schmitt, Martin, and Lüttge, 1989). Clearly, most Type 5 bromeliads must reconcile both gas exchange and water acquisition through the same surface, relying on temporal separation of these two processes by performing gas exchange when the leaf is dry. In contrast, Type 1 and Type 2 bromeliads separate the processes of gas exchange and water acquisition spatially between roots and leaves and tank-forming species between the leaf sheath and blade. Thus, these latter life forms do not need to compromise carbon gain to acquire water. In this respect, wettable trichomes on the leaf blade would not only be an unnecessary investment but would be disadvantageous in mesic habitats, whereas repellent trichomes would favor gas exchange, as perhaps demonstrated by *Pitcairnia macrochlamys* (Benzing, Seemann, and Renfrow, 1978).

Sources of water that may moisten the underside of the leaf may include dew and, perhaps more importantly in cloud forests, wind-borne mist. These factors in conjunction with the terrestrial lifestyle (i.e., the close proximity of vegetation and/or the ground surface from which rainwater can splash upwards onto the underside of the leaf) may help explain the evolution of hydrophobic trichome layers in Bromeliaceae. Indeed, in the family as a whole, rosulate habits typical of genera such as *Fosterella* and *Cryptanthus* tend to have hydrophobic abaxial surfaces (Table 3). Also, terrestrial *Orthophytum benzingii* has basal leaves close to the substrate that possess a repellent trichome layer on the abaxial surface, but on cauline leaves this layer is less apparent (personal observation).

Trichome evolution—The mechanism of water repellency outlined above accords with the scheme of trichome structural evolution detailed by Benzing (1980). In this scheme, the hypothetical ancestral morphology is stellate (the simple filamentous trichomes of some *Navia* species appear to be derived; Benzing, 1980; Terry, Brown, and Olmstead, 1997). Low densities of stellate trichomes provide only discontinuous, patchy repellency (e.g., extant *Pitcairnia arcuata*), increased densities of which would maintain a greater proportion of the moistened leaf surface dry. Following this proposed early increase in trichome density, stellate trichomes may then have undergone an increase in the number of ring cells, becoming truly peltate. This would increase the area covered by each trichome and thereby foster the ''lifting'' mechanism of repellency (high densities of intermediate stellate/ring-peltate trichomes occur in *Pitcairnia corallina* and *P. integrifolia* [Figs. 10, 31] and *P. macrochlamys*; Benzing, Seemann, and Renfrow, 1978). Additionally, the extrusive ring cells of such peltate trichomes appear to lend the overall surface an extremely irregular small-scale texture (e.g., Figs. 29–31).

Hydrophilic trichome layers among extant Bromelioideae feature lower trichome densities, suggesting a decline in trichome density from ancestors with dense hydrophobic layers. This perhaps reflects adaptive radiation into less crowded or relatively xeric niches. Indeed, Type 1 *Ronnbergia explodens* has dense hydrophobic trichome layers and grows in the understory of cloud forest habitats (Figs. 36, 37; Table 3). More xeromorphic terrestrial species (CAM equipped and succulent) such as *Cryptanthus warasii* and *C. whitmanii* may possess hydrophilic surfaces characterized by fewer trichomes (Fig. 38; Table 3; unpublished data), as do many Type 3 species (*Aechmea dactylina, A. nudicaulis*; Figs. 1, 2, 34, 40; Table 3).

Dense trichome layers in Tillandsioideae are usually hydrophilic, unlike those of Bromelioideae and Pitcairnioideae. Indeed, Billings (1904) points out that one of the most unusual features of *Tillandsia usneoides* is that ''unlike most similar appendages of the epidermis, the scales do not hinder the leaf from becoming wet.'' Dense hydrophilic trichome layers in Tillandsioideae must possess a difference that can account for their lack of water repellency. At present, differences in the chemical composition of these surfaces cannot be ruled out. However, a striking structural difference between the trichomes of Tillandsioideae and those of the other subfamilies is apparent, which could also explain the different interaction with water. From scanning electron micrographs published in other sources (Benzing, Seemann, and Renfrow, 1978; Benzing, 1980; Adams and Martin, 1986), it is possible to see that the parts of adjacent tillandsioid trichomes that overlap one another are the flexible wings, which overlap when flattened (wet). Thus, when the leaf is dry and the wings are flexed upwards, underlying epidermis cells are exposed (Benzing,

TABLE 3. Leaf blade surface–water interactions of species of the family Bromeliaceae, divided by subfamily. Adaxial and abaxial surfaces were either intact (surface structures present) or denuded (surface structures removed). Surface type—hydrophilic, hydrophobic, or not significantly interactive (nsi)—is denoted by the depth of a 10-μL droplet of aqueous fluorochrome after a period of 40 min compared between intact and denuded surfaces. Depth values are derived from fluorochrome luminosity (under exciting UV) compared against standards of measured droplet depth (fluorochrome on paraplast wax and glass surfaces). Values represent means ± 1 SE of four replicates (* denotes species of which six replicates were used). Different letters (a–b) represent significant differences between intact and denuded means at the $P \leq 0.05$ level as determined by Student's *t* test. The photosynthetic carbon assimilation pathway (C_3 or crassulacean acid metabolism) employed by each species was determined by ΔH^+, if not previously disclosed by Martin (†; 1994) and references therein, or determined via carbon isotope discrimination by Crayn, Winter, and Smith (‡; unpublished data). Plant material originated from the following countries: AR = Argentina, BO = Bolivia, BR = Brazil, CO = Colombia, CR = Costa Rica, CU = Cuba, DO = Dominica, EC = Ecuador, GT = Guatemala, GY = Guyana, HO = Honduras, JA = Jamaica, ME = Mexico, PA = Panama, PE = Peru, PG = Paraguay, TR = Trinidad, VE = Venezuela. Life forms or ecophysiological types follow the classification of Benzing (2000).

Species	Origin of material	Life form	Carbon pathway	Surface	Depth of droplet (μm) Surface intact	Surface denuded	Surface type
SUBFAMILY PITCAIRNIOIDEAE							
Brocchinia cf. *acuminata* L.B. Smith	VE, Gran Sabana, Sierra de Lema.	4	C_3†	adaxial	284.8 ± 34.6 a	531.2 ± 74.5 b	hydrophilic
				abaxial	706.4 ± 58.9 a	635.2 ± 40.9 a	nsi
Brocchinia gilmartiniae G.S. Varadarajan	VE, La Escalera (1000 m a.s.l.).	4	C_3‡	adaxial	446.4 ± 45.6 a	478.1 ± 18.7 a	nsi
				abaxial	935.1 ± 58.7 b	663.6 ± 32.2 a	hydrophobic (wax)
Brocchinia cf. *hechtioides* Mez	VE, Kavaneyen.	4	C_3‡	adaxial	964.4 ± 18.5 b	672.8 ± 31.9 a	hydrophobic (wax)
				abaxial	895.9 ± 64.3 b	708.5 ± 19.4 a	hydrophobic (wax)
Brocchinia micrantha (Baker) Mez	GY, Kaiteur Falls.	4	C_3†	adaxial	476.4 ± 33.9 a	514.8 ± 56.9 a	nsi
				abaxial	460.0 ± 26.8 a	492.9 ± 34.0 a	nsi
Brocchinia reducta Baker	VE, Hacienda Santa Elena (300 m a.s.l.).	4	C_3†	adaxial	982.2 ± 24.3 b	512.2 ± 90.2 a	hydrophobic (wax)
				abaxial	940.6 ± 25.9 b	625.2 ± 58.5 a	hydrophobic (wax)
Deuterocohnia schreiteri A. Castellanos	AR, *sin loc.*	1	CAM‡	adaxial	451.9 ± 49.7 a	351.9 ± 87.4 a	nsi
				abaxial	947.8 ± 47.9 b	699.9 ± 34.3 a	hydrophobic (trichome)
Dyckia marnier-lapostollei L.B. Smith	BR, Est. Minas Gerais, Diamantiana.	1	CAM‡	adaxial	32.5 ± 102.2 a	489.3 ± 54.4 b	hydrophilic
				abaxial	1417.9 ± 22.5 b	809.1 ± 69.1 a	hydrophobic (trichome)
Dyckia microcalyx Baker	PG, Dpto. Paraguari, Cerro Acahay (450 m a.s.l.).	1	CAM‡	adaxial	631.8 ± 22.2 a	678.0 ± 39.0 a	nsi
				abaxial	379.8 ± 57.2 a	388.2 ± 65.4 a	nsi
Fosterella albicans (Grisebach) L.B. Smith	BO, Dpto. La Paz, Prov. Nor Yungas (800 m a.s.l.).	1	C_3‡	adaxial	454.5 ± 45.9 a	498.3 ± 64.7 a	nsi
				abaxial	1171.7 ± 25.3 b	777.5 ± 110.2 a	hydrophobic (trichome)
Fosterella caulescens Rauh	BO, *sin loc.*	1	C_3‡	adaxial	512.8 ± 65.7 a	456.3 ± 47.9 a	nsi
				abaxial	952.2 ± 14.9 b	665.1 ± 41.0 a	hydrophobic (trichome)
Fosterella cf. *elata* H. Luther	BO, Dpto. La Paz, Prov. Nor Yungas (880 m a.s.l.).	1	C_3‡	adaxial	250.6 ± 50.6 a	360.1 ± 70.2 a	nsi
				abaxial	899.9 ± 12.9 b	628.1 ± 48.7 a	hydrophobic (trichome)
Fosterella petiolata (Mez) L.B. Smith	BO, Dpto. La Paz, Puente Villa, Puenta de Coripata (1200 m a.s.l.).	1	C_3‡	adaxial	728.2 ± 96.9 a	662.5 ± 81.1 a	nsi
				abaxial	1226.5 ± 68.4 b	897.9 ± 42.4 a	hydrophobic (trichome)
Fosterella schidosperma (Baker) L.B. Smith	BO, *sin loc.*	1	C_3‡	adaxial	232.8 ± 53.7 a	409.2 ± 71.4 a	nsi
				abaxial	858.6 ± 59.8 b	623.4 ± 39.9 a	hydrophobic (trichome)
Fosterella sp. nov.	BO, Dpto. La Paz, Prov. Munecas, Consata (1200 m a.s.l.).	1	—	adaxial	506.1 ± 44.1 a	484.6 ± 109.8 a	nsi
				abaxial	523.3 ± 68.6 a	544.8 ± 70.2 a	nsi
Hechtia guatemalensis Mez	HO, Teguicigalpa-Comayagua (1300 m a.s.l.).	1	CAM‡	adaxial	192.0 ± 69.7 a	504.7 ± 40.3 b	hydrophilic
				abaxial	1318.9 ± 34.7 b	911.8 ± 88.5 a	hydrophobic (trichome)
Pitcairnia arcuata (André) André	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	1	C_3	adaxial	1030.3 ± 42.6 b	714.3 ± 60.2 a	hydrophobic (trichome)
				abaxial	832.5 ± 45.4 a	875.5 ± 76.6 a	nsi
Pitcairnia atrorubens (Beer) Baker	CR, Prov. Cartago, La Suiza (1000 m a.s.l.).	1	C_3‡	adaxial	211.8 ± 14.6 a	274.8 ± 46.7 a	nsi
				abaxial	484.8 ± 46.2 a	581.4 ± 68.1 a	nsi
Pitcairnia corallina Linden & André	VE, Edo. Tachira (1200–1500 m a.s.l.).	1	C_3‡	adaxial	628.1 ± 59.6 a	582.8 ± 103.6 a	nsi
				abaxial	899.9 ± 16.7 b	733.8 ± 27.1 a	hydrophobic (trichome)
Pitcairnia echinata Hooker	PE, *sin loc.*	1	C_3‡	adaxial	536.2 ± 44.7 a	605.0 ± 36.1 a	nsi
				abaxial	983.4 ± 8.6 b	777.0 ± 25.8 a	hydrophobic (trichome)
Pitcairnia imbricata (Brongniart) Regel	VE, *sin loc.*	1	C_3‡	adaxial	513.9 ± 24.3 a	510.3 ± 18.9 a	nsi
				abaxial	429.5 ± 40.0 a	543.4 ± 28.4 a	nsi
Pitcairnia integrifolia Ker-Gawler*	TR, Point Gourde, seasonally dry.	1	C_3†	adaxial	258.6 ± 25.2 a	306.9 ± 13.5 a	nsi
				abaxial	718.9 ± 17.8 b	482.8 ± 20.9 a	hydrophobic (trichome)

TABLE 3. Continued.

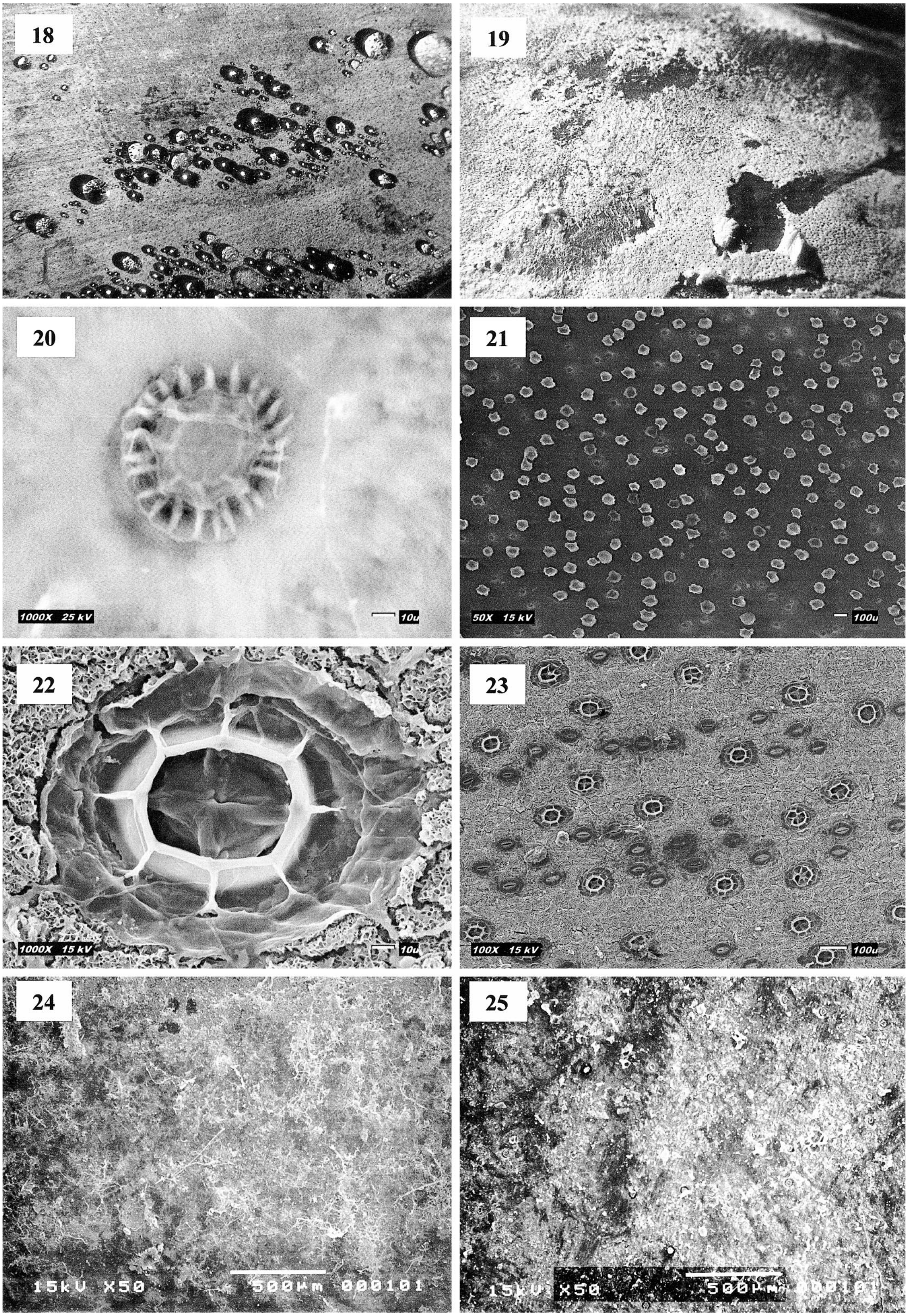
Species	Origin of material	Life form	Carbon pathway	Surface	Depth of droplet (μm) Surface intact	Depth of droplet (μm) Surface denuded	Surface type
Pitcairnia maidifolia (C. Morren) Decaisne	PE, Dpto. San Martin, Tarapoto-Yurimaguas (1000 m a.s.l.).	1	C_3‡	adaxial	444.2 ± 12.7 a	521.3 ± 61.6 a	nsi
				abaxial	495.6 ± 55.6 a	591.2 ± 51.8 a	nsi
Pitcairnia microtrinensis R.W. Read	DO (1250 m a.s.l.).	1	C_3‡	adaxial	295.4 ± 74.5 a	441.6 ± 66.6 a	nsi
				abaxial	630.8 ± 30.6 a	648.0 ± 18.6 a	nsi
Pitcairnia palmoides Mez & Sodiro	EC, Prov. Carchi, Chical (1300 m a.s.l.).	1	C_3‡	adaxial	497.3 ± 44.6 a	553.8 ± 34.0 a	nsi
				abaxial	794.8 ± 52.2 a	791.8 ± 39.8 a	nsi
Pitcairnia patentiflora L.B. Smith	*Sin loc.*	1	C_3(CAM)‡	adaxial	363.3 ± 33.4 a	363.3 ± 42.0 a	nsi
				abaxial	469.9 ± 21.1 a	510.3 ± 25.5 a	nsi
Pitcairnia recurvata (Scheidweiler) K. Koch	ME, Edo. Veracruz, Playa Escondido.	1	C_3‡	adaxial	476.4 ± 64.1 a	547.6 ± 34.0 a	nsi
				abaxial	1286.7 ± 38.3 b	865.1 ± 28.3 a	hydrophobic (trichome)
Pitcairnia riparia Mez	EC, Morona-Santiago.	1	C_3‡	adaxial	464.7 ± 58.0 a	495.4 ± 53.6 a	nsi
				abaxial	483.1 ± 34.8 a	520.0 ± 40.8 a	nsi
Pitcairnia rubronigriflora Rauh	PE, Dpto. San Martin, Tarapoto (1000 m a.s.l.).	1	C_3‡	adaxial	522.4 ± 22.3 a	546.0 ± 56.7 a	nsi
				abaxial	658.1 ± 68.1 a	711.2 ± 62.7 a	nsi
Pitcairnia undulata Scheidweiler	ME, Edo. Chiapas.	1	C_3‡	adaxial	315.5 ± 12.6 a	392.7 ± 23.2 b	hydrophilic
				abaxial	844.7 ± 39.1 b	679.4 ± 24.4 a	hydrophobic (trichome)
Pitcairnia unilateralis L.B. Smith	EC, Prov. Manabi.	1	C_3‡	adaxial	382.7 ± 68.4 a	484.6 ± 89.6 a	nsi
				abaxial	892.3 ± 9.5 b	714.9 ± 38.0 a	hydrophobic (trichome)
Pitcairnia valerii Standley	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	1	C_3‡	adaxial	647.4 ± 70.6 a	618.5 ± 119 a	nsi
				abaxial	555.8 ± 24.3 a	758.4 ± 86.7 a	nsi
Puya ctenorhyncha L.B. Smith	BO, Dpto. La Paz, Prov. Larecaja, Cerro Iminapi, Sorata (2680 m a.s.l.).	1	CAM‡	adaxial	240.0 ± 27.3 a	316.1 ± 40.3 a	nsi
				abaxial	454.5 ± 83.1 a	446.7 ± 36.9 a	nsi
Puya lanata Kunth	*Sin loc.*	1	CAM‡	adaxial	14.7 ± 8.6 a	232.2 ± 35.2 b	hydrophilic
				abaxial	70.7 ± 70.7 a	347.3 ± 38.3 b	hydrophilic
Puya laxa L.B. Smith	Old hort. plant.	1	CAM‡	adaxial	563.1 ± 105.9 a	489.3 ± 15.5 a	nsi
				abaxial	538.5 ± 82.4 a	624.6 ± 29.1 a	nsi
SUBFAMILY TILLANDSIOIDEAE							
Alcantarea cf. *odorata* (Leme) J.R. Grant	BR, *sin loc.*	4	C_3(CAM)‡	adaxial	926.1 ± 35.8 b	638.9 ± 52.9 a	hydrophobic (wax)
				abaxial	1073.9 ± 4.4 b	747.7 ± 52.7 a	hydrophobic (wax)
Catopsis micrantha L.B. Smith	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	1870.5 ± 149.2 b	1072.5 ± 7.2 a	hydrophobic (wax)
				abaxial	1971.5 ± 32.8 b	1009.3 ± 71.7 a	hydrophobic (wax)
Catopsis nitida (Hooker) Grisebach	PA, Prov. Chiriqui, Fortuna, lower montane wet forest (1200 m a.s.l.).	4	C_3	adaxial	618.9 ± 15.8 a	673.7 ± 35.5 a	nsi
				abaxial	640.8 ± 19.3 a	607.9 ± 13.8 a	nsi
Catopsis nutans (Swartz) Grisebach	HO, Prov. Cortes, San Pedro, Sula (100 m a.s.l.).	4	C_3(CAM)†	adaxial	854.2 ± 48.2 b	569.5 ± 19.9 a	hydrophobic (wax)
				abaxial	427.2 ± 47.7 a	465.5 ± 41.3 a	nsi
Catopsis sessiliflora (Ruiz & Pavon) Mez	BO, Dpto. La Paz, Prov. Larecaja, Tipuani-Caranavi (1250 m a.s.l.).	4	C_3†	adaxial	958.2 ± 30.2 b	690.0 ± 19.9 a	hydrophobic (wax)
				abaxial	547.6 ± 8.9 a	498.3 ± 54.7 a	nsi
Catopsis subulata L.B. Smith	GT, bought in market in Guatemala City.	4	C_3‡	adaxial	422.9 ± 53.9 a	503.2 ± 70.6 a	nsi
				abaxial	824.5 ± 7.5 b	684.7 ± 29.9 a	hydrophobic (wax)
Guzmania circinnata Rauh	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	848.2 ± 70.9 a	822.8 ± 92.6 a	nsi
				abaxial	831.3 ± 44.4 a	915.8 ± 88.8 a	nsi
Guzmania coriostachya (Grisebach) Mez	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	671.6 ± 16.7 a	743.9 ± 28.8 a	nsi
				abaxial	686.0 ± 29.9 a	753.6 ± 48.2 a	nsi
Guzmania macropoda L.B. Smith	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3‡	adaxial	342.7 ± 9.4 a	353.9 ± 18.2 a	nsi
				abaxial	737.6 ± 11.2 b	521.5 ± 45.7 a	hydrophobic (wax)
Guzmania monostachia (L.) Rusby ex Mez. var. *monostachia**	PA, Coclé province, Mata Ahogado, montane wet forest (1000 m a.s.l.).	4	C_3-CAM†	adaxial	662.3 ± 86.6 a	814.4 ± 68.1 a	nsi
				abaxial	890.4 ± 119.5 a	991.8 ± 107.8 a	nsi
Guzmania musaica (Linden & André) Mez var. *musaica*	PA, Prov. Chiriqui, Fortuna, lower montane wet forest (1200 m a.s.l.).	4	C_3†	adaxial	597.0 ± 22.7 a	702.9 ± 75.5 a	nsi
				abaxial	604.3 ± 10.3 a	618.9 ± 15.8 a	nsi

TABLE 3. Continued.

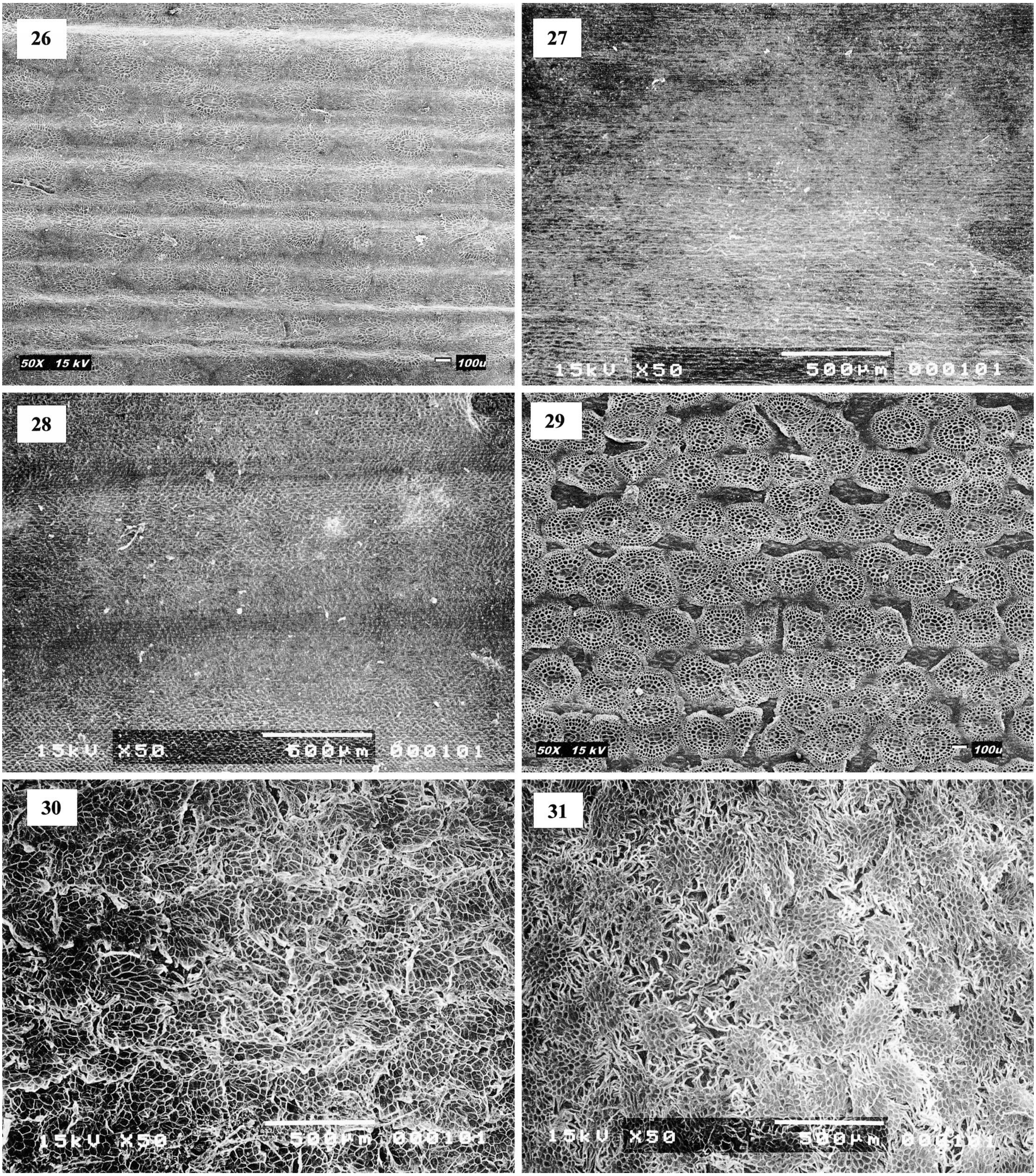
Species	Origin of material	Life form	Carbon pathway	Surface	Depth of droplet (μm) Surface intact	Depth of droplet (μm) Surface denuded	Surface type
Guzmania musaica (Linden & André) Mez *var. discolor* H. Luther	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	663.3 ± 44.2 a	741.8 ± 63.3 a	nsi
				abaxial	551.8 ± 36.1 a	519.0 ± 105.9 a	nsi
Guzmania retusa L.B. Smith	PE, Dpto. San Martin, Tarapoto-Yurimaguas (1200 m a.s.l.).	4	C_3‡	adaxial	476.4 ± 72.7 a	308.4 ± 45.7 a	nsi
				abaxial	955.2 ± 21.0 b	350.4 ± 86.9 a	hydrophobic (wax)
Racinaea spiculosa (Grisebach) M.A. Spencer & L.B. Smith var. *spiculosa*	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	842.8 ± 92.2 a	993.8 ± 57.1 a	nsi
				abaxial	901.8 ± 18.8 a	983.5 ± 43.1 a	nsi
Tillandsia cauligera Mez	PE, Dpto. Qosqo, Ollantaytambo, saxicolous (2700 m a.s.l.).	4–5	CAM‡	adaxial	5.7 ± 5.9 a	414.5 ± 147.6 b	hydrophilic
				abaxial	199.2 ± 165.5 a	659.1 ± 48.9 b	hydrophilic
Tillandsia elongata Kunth var. *subimbricata* (Baker) L.B. Smith	PA, Prov. Panamá, Gamboa, lowland seasonally dry forest.	4	CAM†	adaxial	817.5 ± 22.4 a	1028.0 ± 40.4 b	hydrophilic
				abaxial	768.3 ± 31.3 a	958.5 ± 37.6 b	hydrophilic
Tillandsia flexuosa Swartz*	PA, Prov. Panamá, Panama City, Cerro Ancon, lowland urban, seasonally dry.	4–5	CAM†	adaxial	349.0 ± 79.2 a	641.4 ± 10.8 b	hydrophilic
				abaxial	334.1 ± 111.3 a	593.8 ± 14.2 b	hydrophilic
Tillandsia nana Baker	PE, Dpto. Qosqo, Ollantaytambo, seasonally dry, saxicolous on rock-faces (2700 m a.s.l.).	5	CAM‡	adaxial	0.0 ± 0.0 a	732.1 ± 36.4 b	hydrophilic
				abaxial	9.4 ± 120.9 a	885.4 ± 40.6 b	hydrophilic
Tillandisia stricta Solander var. *stricta*	TR, *sin loc.*	5	CAM†	adaxial	0.0 ± 0.0 a	321.3 ± 49.7 b	hydrophilic
				abaxial	25.1 ± 54.0 a	579.4 ± 57.7 b	hydrophilic
Vriesea monstrum (Mez) L.B. Smith	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	833.5 ± 44.6 a	771.0 ± 105.3 a	nsi
				abaxial	938.3 ± 17.1 b	714.8 ± 54.9 a	hydrophobic (trichome)
Werauhia capitata (Mez & Wercklé) J.R. Grant	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	831.3 ± 46.7 a	804.3 ± 46.7 a	nsi
				abaxial	915.5 ± 72.0 b	562.0 ± 65.9 a	hydrophobic (wax)
Werauhia gladioliflora (Wendland) J.R. Grant	ME, Edo. Chiapas (1000 m a.s.l.).	4	C_3‡	adaxial	268.7 ± 87.5 a	528.3 ± 103.9 a	nsi
				abaxial	451.6 ± 27.9 a	540.1 ± 58.6 a	nsi
Werauhia hygrometrica (André) J.R. Grant	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	885.5 ± 51.7 a	869.5 ± 96.4 a	nsi
				abaxial	1039.5 ± 68.9 a	875.0 ± 21.9 a	nsi
Werauhia panamaensis (E. Gross & Rauh) J.R. Grant	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	786.8 ± 52.8 a	825.3 ± 49.2 a	nsi
				abaxial	564.5 ± 83.9 a	641.0 ± 53.8 a	nsi
Werauhia sanguinolenta (Linden ex Cogniaux & Marchal) J.R. Grant	PA, Prov. Panamá, Gamboa, lowland seasonally dry forest,	4	C_3	adaxial	911.8 ± 45.7 a	966.0 ± 54.1 a	nsi
				abaxial	1020.8 ± 28.6 a	1038.0 ± 34.0 a	nsi
Werauhia vittata (Mez & Wercklé) J.R. Grant	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	4	C_3	adaxial	859.0 ± 59.5 a	918.8 ± 52.3 a	nsi
				abaxial	810.0 ± 94.9 a	892.5 ± 36.4 a	nsi
SUBFAMILY BROMELIOIDEAE							
Aechmea dactylina Baker*	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	3	CAM	adaxial	490.2 ± 56.7 a	709.3 ± 18.7 b	hydrophilic
				abaxial	515.5 ± 14.5 a	647.2 ± 22.2 b	hydrophilic
Aechmea fasciata (Lindley) Baker	BR, *sin loc.*	3	CAM‡	adaxial	617.5 ± 24.5 a	602.3 ± 38.1 a	nsi
				abaxial	795.9 ± 41.7 b	587.2 ± 20.9 a	hydrophobic (trichome)
Aechmea fendleri André ex Mez	TR, Textel, transitional montane forest (710 m a.s.l.)	3	CAM†	adaxial	341.2 ± 38.7 a	477.3 ± 20.4 b	hydrophilic
				abaxial	489.4 ± 45.0 a	601.3 ± 37.9 b	hydrophilic
Aechmea magdalenae (André) André ex Baker*	PA, Prov. Panamá, Barro Colorado Island, shaded understory.	2	CAM†	adaxial	310.5 ± 86.4 a	523.5 ± 54.3 b	hydrophilic
				abaxial	591.0 ± 61.6 a	606.7 ± 46.1 a	nsi
Aechmea nudicaulis (L.) Grisebach	PA, Prov. Bocas del Toro, Chiriqui Grande (3 m a.s.l.).	3	CAM†	adaxial	211.1 ± 10.5 a	478.1 ± 64.5 b	hydrophilic
				abaxial	740.5 ± 77.3 b	514.3 ± 46.9 a	hydrophobic (trichome)
Aechmea veitchii Baker*	PA, Prov. Chiriqui, Fortuna, lower montane wet forest (1200 m a.s.l.).	1	C_3‡	adaxial	605.6 ± 47.7 a	671.4 ± 43.1 a	nsi
				abaxial	1050.3 ± 11.9 b	853.1 ± 24.5 a	hydrophobic (trichome)
Ananas comosus (L.) Merril cv. Cayenne Lisse*	Agricultural clone.	2	CAM	adaxial	619.5 ± 36.5 a	667.7 ± 11.0 a	nsi
				abaxial	842.2 ± 13.2 b	685.3 ± 12.4 a	hydrophobic (trichome)
Billbergia macrolepis L.B. Smith	PA, Prov. Panamá, Gamboa, lowland seasonally dry forest.	2–3	CAM	adaxial	438.3 ± 108.2 a	498.8 ± 22.9 a	nsi
				abaxial	1130.3 ± 16.6 b	341.8 ± 116.1 a	hydrophobic (trichome)

TABLE 3. Continued.

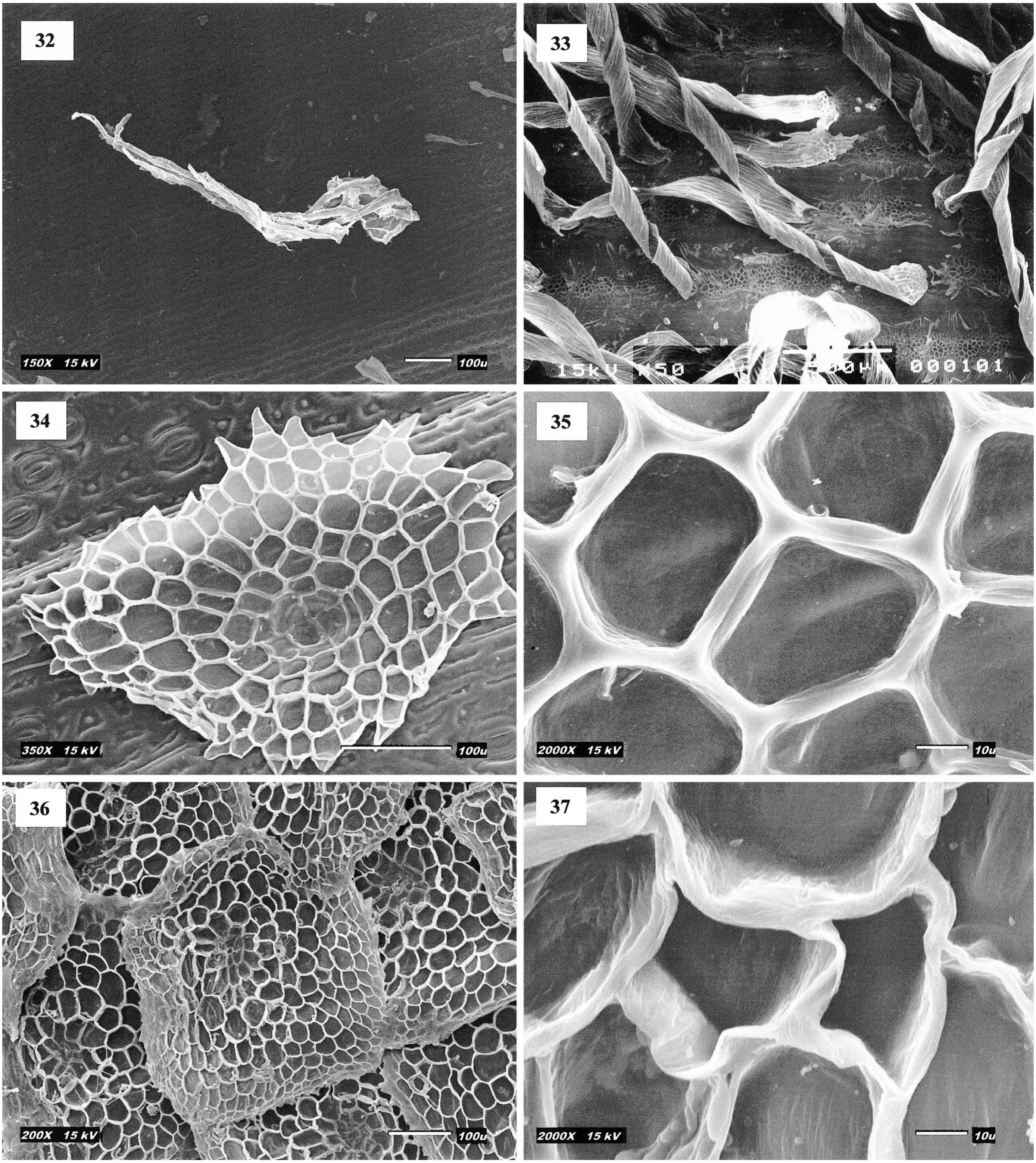
Species	Origin of material	Life form	Carbon pathway	Surface	Depth of droplet (μm) Surface intact	Depth of droplet (μm) Surface denuded	Surface type
Billbergia robert-readii E. Gross & Rauh	PE, Dpto. Madre de Dios, Hacienda Salvación, near Quincemil, epiphytic in forest.	3	CAM‡	adaxial	256.6 ± 116.6 a	681.2 ± 51.7 b	hydrophilic
				abaxial	1009.3 ± 43.9 b	589.5 ± 114.5 a	hydrophobic (trichome)
Billbergia rosea Hortus ex Beer	VE, *sin loc.* (Distribution: VE–TR).	3	CAM†	adaxial	233.3 ± 74.9 a	541.8 ± 13.4 b	hydrophilic
				abaxial	578.1 ± 28.9 a	611.4 ± 17.8 a	nsi
Billbergia stenopetala Harms	EC, Prov. Napo, Tulag.	3	CAM‡	adaxial	386.1 ± 223.7 a	358.5 ± 125.4 a	nsi
				abaxial	786.3 ± 31.6 b	479.2 ± 52.5 a	hydrophobic (trichome)
Bromelia pinguin L.*	PA, Prov. Panamá, Cerro Azul, tropical wet forest (691 m a.s.l.).	2	CAM†	adaxial	725.8 ± 43.6 a	788.5 ± 22.5 a	nsi
				abaxial	761.3 ± 60.2 a	795.2 ± 53.0 a	nsi
Canistrum seidelianum Weber	BR, *ex hort.*	3	CAM‡	adaxial	169.8 ± 62.9 a	426.9 ± 51.2 b	hydrophilic
				abaxial	75.9 ± 54.7 a	535.8 ± 29.8 b	hydrophilic
Cryptanthus cf. *bromelioides* Otto & Dietrich	BR, Est. Rio de Janeiro, Barra de Tijuca, dense forest on hillside, clay and leaf-litter substrate (30 m a.s.l.).	1	CAM‡	adaxial	0.0 ± 0.0 a	388.8 ± 49.3 b	hydrophilic
				abaxial	646.1 ± 58.6 a	761.1 ± 35.1 a	nsi
Cryptanthus dianae Leme	BR, Est. Espirito Santo, Presidente Kennedy, Praia de Maroba.	1	CAM‡	adaxial	18.6 ± 15.5 a	134.7 ± 18.9 b	hydrophilic
				abaxial	513.0 ± 33.3 b	343.4 ± 57.4 a	hydrophobic (trichome)
Cryptanthus glaziovii Mez	BR, Est. Minas Gerais, Caraca (1000–1200 m a.s.l.).	1	C_3‡	adaxial	360.4 ± 50.3 a	378.5 ± 51.9 a	nsi
				abaxial	763.2 ± 47.6 a	817.5 ± 30.9 a	nsi
Cryptanthus warasii E. Pereira	BR, Edo. Minas Gerais, vic. Diamantina.	1	CAM‡	adaxial	0.0 ± 0.0 a	631.9 ± 65.8 b	hydrophilic
				abaxial	998.5 ± 37.3 b	781.3 ± 11.7 a	hydrophobic (trichome)
Cryptanthus whitmanii Leme	BR, Est. Espirito Santo, Domingos Martins.	1	—	adaxial	177.6 ± 61.2 a	382.7 ± 44.5 b	hydrophilic
				abaxial	782.9 ± 17.9 b	375.2 ± 49.9 a	hydrophobic (trichome)
Hohenbergia pendulaflora (A. Richard) Mez	West Indies, *sin loc.*	3	CAM‡	adaxial	363.1 ± 99.4 a	770.2 ± 83.6 b	hydrophilic
				abaxial	994.4 ± 41.3 a	882.3 ± 49.6 a	nsi
Neoregelia cruenta (R. Graham) L.B. Smith*	BR, Est. Rio de Janeiro, near sea level.	3	CAM†	adaxial	562.0 ± 44.9 a	543.9 ± 47.7 a	nsi
				abaxial	608.4 ± 36.8 a	582.2 ± 37.9 a	nsi
Orthophytum benzingii Leme & H. Luther	BR, Est. Minas Gerais, lithophyte, partial shade (450 m a.s.l.).	1	C_3(CAM)‡	adaxial	0.0 ± 0.0 a	477.0 ± 38.1 b	hydrophilic
				abaxial	1079.7 ± 97.6 b	606.1 ± 76.5 a	hydrophobic (trichome)
Orthophytum gurkenii Hutchison	BR, *sin loc.*	1	CAM‡	adaxial	47.7 ± 47.7 a	286.6 ± 27.0 b	hydrophilic
				abaxial	138.9 ± 111.9 a	438.9 ± 38.5 b	hydrophilic
Orthophytum magalhaesii L.B. Smith	BR, Est. Bahia.	1	CAM‡	adaxial	0.0 ± 0.0 a	286.8 ± 94.2 b	hydrophilic
				abaxial	0.0 ± 0.0 a	265.3 ± 87.8 b	hydrophilic
Quesnelia blanda (Schott ex Beer) Mez	BR, Est. Rio de Janeiro.	3	CAM‡	adaxial	330.1 ± 39.9 a	523.7 ± 10.3 b	hydrophilic
				abaxial	420.8 ± 47.5 a	626.5 ± 9.1 b	hydrophilic
Quesnelia marmorata (Lemaire) R.W. Read cv. Tim Plowman	BR, Est. Rio de Janeiro, Rio Bonito.	3	CAM†	adaxial	503.4 ± 76.5 a	558.6 ± 48.9 a	nsi
				abaxial	727.6 ± 42.9 a	648.3 ± 37.1 a	nsi
Ronnbergia explodens L.B. Smith	PA, Prov. Panamá, Cerro Jefe, elfin cloud forest (1007 m a.s.l.).	1	C_3	adaxial	275.7 ± 51.4 a	420.95 ± 41.0 a	nsi
				abaxial	666.8 ± 13.6 b	566.2 ± 36.7 a	hydrophobic (trichome)



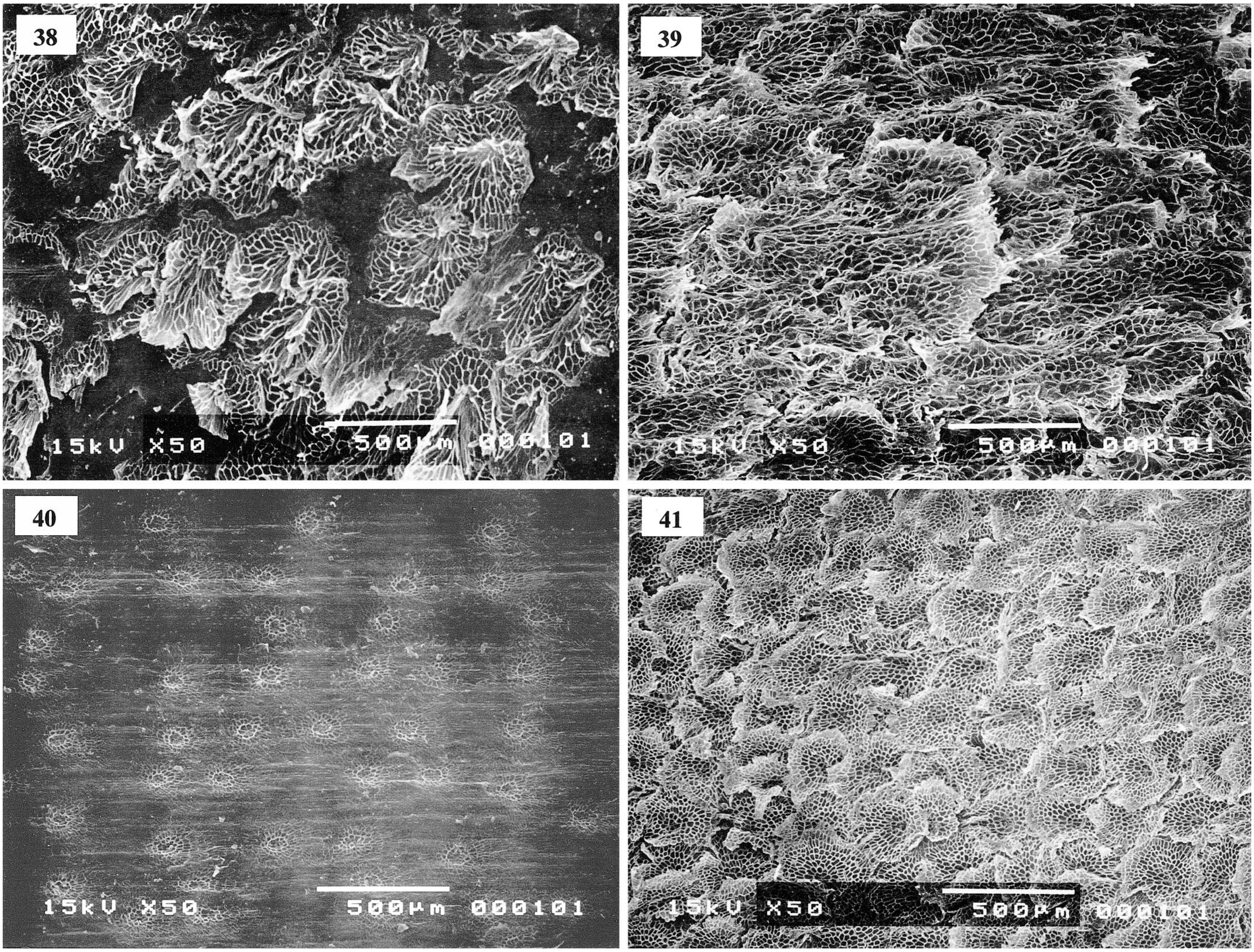
Figs. 18–25. Epicuticular wax powder layers of leaf blade surfaces of bromeliads. **18.** *Catopsis micrantha,* photograph of water droplets on adaxial surface of leaf blade. **19.** *Catopsis micrantha,* photograph of epicuticular wax powder layer on abaxial surface of leaf sheath. **20.** *Catopsis micrantha,* scanning electron micrograph (SEM) of trichome embedded in wax layer (unprepared specimen). **21.** *Catopsis micrantha,* SEM of trichomes on the wax-free adaxial leaf sheath surface (prepared specimen). **22.** *Werauhia capitata,* SEM of trichome on abaxial surface. **23.** *Werauhia capitata,* SEM of abaxial surface. **24.** *Alcantarea odorata,* SEM of adaxial surface, **25.** *Brocchinia reducta,* SEM of adaxial surface.



Figs. 26–31. Scanning electron micrographs of bromeliad leaf blade surfaces, the adaxial surfaces of which do not interact with water, the abaxial surfaces hydrophobic. **26–28.** Noninteractive adaxial surfaces of *Vriesea monstrum, Fosterella petiolata* and *Pitcairnia corallina,* respectively, lacking trichomes or with filmy trichomes. **29–31.** Hydrophobic abaxial surfaces of *Vriesea monstrum, Fosterella petiolata,* and *Pitcairnia corallina,* respectively, with well-defined trichomes in a confluent layer.



Figs. 32–37. Scanning electron micrographs of trichomes from bromeliad leaf blade surfaces, the indumenta of which have different interactions with water. **32.** *Pitcairnia arcuata,* attenuated stellate trichome with radial filaments tangled together, low densities of which form a hydrophobic indumentum. **33.** *Puya laxa* has two types of trichome, one peltate and the other with a grossly elongate wing that spirals around itself to form a hair-like structure, the indumentum having no interaction with water. **34.** *Aechmea dactylina,* peltate trichome in a hydrophilic indumentum. **35.** *Aechmea dactylina,* detail of trichome shield. **36.** *Ronnbergia explodens,* peltate trichome in a hydrophobic indumentum. **37.** *Ronnbergia explodens,* detail of trichome shield.



Figs. 38–41. Scanning electron micrographs of trichomes on hydrophilic and hydrophobic surfaces of the same leaf blade. **38–39.** *Cryptanthus whitmanii*, hydrophilic adaxial and hydrophobic abaxial surfaces, respectively. **40–41.** *Aechmea nudicaulis*, hydrophilic adaxial and hydrophobic abaxial surfaces, respectively.

TABLE 4. The effect of removal of water surface tension on the leaf blade trichome-layer–water interactions of *Ananas comosus*. Repellency was denoted by the depth of a 10-µL droplet of aqueous fluorochrome after a period of 40 min. The fluorochrome used was either fluorescein sodium solution (5 mL of 0.05% fluorescein + 0.5 mL H_2O) or a solution of fluorescein and household detergent (5 mL of 0.05% fluorescein + 0.5 mL neat detergent). Depth values are derived from fluorochrome luminosity (under exciting UV light) compared against standards of measured droplet depth (fluorochrome on paraplast wax and glass surfaces). Values represent means ± 1 SE of six replicates. Different letters (a–c) represent significant differences between means at the $P \leq 0.05$ level as determined by Tukey's multiple comparison procedure (ANOVA).

Leaf blade surface	Depth of aqueous droplet (µm)	
	Fluorochrome	Fluorochrome + detergent
Adaxial	559.3 ± 81.6 b	14.8 ± 3.2 a
Abaxial	1013.1 ± 41.7 c	17.6 ± 5.3 a

Seemann, and Renfrow, 1978). When the leaf is wetted, surface tension forces acting on the epidermis and/or the underside of the trichome wing may permit water to spread. Thus, dense trichome layers in most Tillandsioideae have different configurations when wet and dry and will only form a confluent layer after wetting. The moveable trichome wing of the Type 5 life form may therefore be regarded as a device allowing the presence of high densities of trichomes while avoiding repellency.

Indeed, dense layers of peltate trichomes that lack wings in Tillandsioideae are hydrophobic (e.g., *Vriesea monstrum*; Fig. 29; Table 3). Also, the immobile trichomes of Type 3 bromeliads demonstrate that a moveable wing is not essential for absorption (Benzing, Givnish, and Bermudes, 1985). The moveable wing is generally associated with higher trichome densities and effective water and nutrient absorption by the leaf surface (Benzing and Burt, 1970).

Epicuticular wax powders—Benzing, Givnish, and Bermudes (1985) suggest that Tillandsioideae and *Brocchinia*—both of which include advanced Type 4 tank forms equipped

TABLE 5. Summary of principal leaf blade interactions with water (as determined by fluorographic dimensional imaging) of the different ecophysiological types of Bromeliaceae. ''Ring-peltate'' trichomes possess a shield composed mainly of ring cells, and ''wing-peltate'' trichomes possess a shield with a moveable wing. Life forms or ecophysiological types follow the classification of Benzing (2000).

Life form	Trichome type	Trichome cover	Interaction with water	Example
1	stellate	discontinuous	hydrophobic	*Pitcairnia arcuata*
	stellate/ring peltate	continuous	hydrophobic	*Fosterella petiolata, Ronnbergia explodens*
	ring-peltate	discontinuous	hydrophilic	*Cryptanthus whitmanii*
2	ring-peltate	continuous	hydrophobic	*Ananas comosus*
	ring-peltate	discontinuous	hydrophilic	*Aechmea magdalenae*
3	ring-peltate	continuous	hydrophobic	*Aechmea nudicaulis*
	ring-peltate	discontinuous	hydrophilic	*Aechmea dactylina*
4	ring-peltate	continuous	hydrophobic	*Vriesea monstrum*
	wing-peltate	continuous	hydrophilic	*Tillandsia elongata*
	wing-peltate	discontinuous	noninteractive	*Werauhia sanguinolenta*
5	wing-peltate	continuous	hydrophilic	*Tillandsia nana*

with absorbent trichomes—are derived from a common ancestor. Indeed, in the present study only Tillandsioideae and *Brocchinia* provided examples of species in which epicuticular wax powders are produced. Waxy *Catopsis* species have been shown to use wing-peltate trichomes to take up mineral ions and amino acids (Benzing et al., 1976; Benzing, 1980; Benzing and Pridgeon, 1983), and this probably also applies to *C. micrantha.* Both leaf surfaces bear a powdery layer of epicuticular wax, and this is also one of the few taxa reported to be amphistomatous (see Tomlinson, 1969; Figs. 13, 14). Thus, extensive epicuticular wax powders appear to have evolved only in taxa containing Type 4 life forms, which use trichomes to acquire water and minerals from tanks.

It is likely that in many Type 4 species a combination of the horizontal orientation of the leaf and the hypostomatous condition are sufficient to keep stomata unobstructed by water; in the present study, predominantly those species that possessed upright leaves (e.g., *Brocchinia reducta, Guzmania macropoda, Werauhia capitata*), and/or stomata on the adaxial surface (*Catopsis micrantha*) possessed hydrophobic wax powders on the leaf blade. Possibly the upright funnelform habit increases the utility of the tank as an impoundment, and tank formers face a trade-off between gas exchange and impoundment capacity, wax powders being a method of maximizing both. Reflective epicuticular wax powders have also been implicated in the attraction and entrapment of insects in a small number of Type 4 bromeliads—*Catopsis berteroniana, Brocchinia hechtioides,* and *B. reducta* (Fish, 1976; Frank and O'Meara, 1984; Givnish et al., 1984; Owen, Benzing, and Thomson, 1988; Owen and Thomson, 1991; Benzing, 2000). It is possible that a slippery and reflective epicuticular wax powder helped predispose these lineages to carnivory.

Conclusions—Hydrophobic leaf surfaces of Bromeliaceae possess a highly irregular microrelief, thereby reducing the adhesion and spread of water on the leaf blade. Hydrophobic trichome layers occur on the abaxial leaf blade surfaces of many mesic Type 1 pitcairnioids and, as these species exhibit the putative primitive ecological condition, water repellency appears to have been an important condition in early Bromeliaceae. The trichomes of Type 4 species are specialized for the alternative function of water and nutrient absorption from a water-filled tank, with epicuticular wax powders employed by some species to shed water from the leaf blades. Hydrophobic trichome layers and wax powders could potentially obstruct pathogens and particulates, aid in self-cleaning, and/or maintain gas exchange during wet weather.

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