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Absorptive Trichomes in *Brocchinia reducta* (Bromeliaceae) and Their Evolutionary and Systematic Significance

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ABSTRACT. *Brocchinia reducta*, a tank-forming member of subfamily Pitcairnioideae (Bromeliaceae), possesses foliar trichomes capable of absorbing ^3H -leucine as do those borne by other members of the same family (all Tillandsioideae and some species of Bromelioideae). In general, pitcairnioid trichomes have been considered incapable of participating in nutrient uptake. Other features of leaf anatomy and physiology, such as the presence of the C3 photosynthetic pathway, suggest that either 1) *Brocchinia* and tillandsioid tank shoots bearing absorptive hairs are a result of convergence or 2) both subfamilies acquired this feature from the same ancestor. All in all, Tillandsioideae and Pitcairnioideae share more vegetative features in common than either does with Bromelioideae and, thus, may be more closely related than was previously suspected. Tank deployment in Bromelioideae seems to have originated independently from a semi-xeric terrestrial habit that incorporated the CAM syndrome. Factors that could have led to the emergence of absorptive trichomes in Bromeliaceae are identified.

Bromeliaceae, an essentially neotropical family of about 2100 species comprising three subfamilies (Smith and Downs 1974, 1977, 1979) has received considerable study over many years. In addition to systematic problems, subjects of great interest have been vegetative features that enable these plants to occupy such disparate habitats as swamps, deserts, and forest canopies. Analyses of adaptations have fostered speculation and controversy, much of which is centered on ancestral bromeliad habitat preferences and interrelationships of subfamilies. Pitcairnioideae are generally viewed as containing the most primitive species in terms of habit, water balance mechanisms, nutrient uptake, and dependence on soil. Epiphytism probably developed in Bromelioideae and Tillandsioideae by different routes.

Central to speculations on bromeliad evolution is the foliar trichome. Depending on the taxon, a foliar indumentum may supplement or fully replace root absorptive function (Benzing and Renfrow 1980). Comparative surveys have led to the belief that trichomes over entire shoots of Tillandsioideae (the tillandsioids) and leaf bases of tank-forming Bromelioideae (the

bromelioids) are absorptive; the foliar appendages borne by members of Pitcairnioideae (the pitcairnioids) are not (Mez 1904; Tietze 1906; Aso 1909; Benzing et al. 1976; Sakai and Sanford 1980; Benzing and Pridgeon 1983). In fact, direct assessments of foliar permeability and, specifically, the involvement of bromeliad trichomes in solute uptake, have been limited to Bromelioideae and Tillandsioideae with the exception of two *Pitcairnia* species (Benzing and Burt 1970; Benzing et al. 1976). Earlier claims (Tietze 1906; Aso 1909) that foliar hairs contribute only marginally, if at all, to nutrient ion procurement in Pitcairnioideae were corroborated. However, definitive judgments on the roles of pitcairnioid trichomes in water balance and nutrient absorption must await a more representative survey of the subfamily. Such a study should certainly include the most likely bearers of absorptive hairs in Pitcairnioideae: taxa of the genus *Brocchinia*.

Brocchinia is a little-studied assemblage of 18 species endemic to the Guayana Highlands of northern South America (Smith and Downs 1974). Some taxa are known from type collections only; many are quite localized, occurring

only on very few tepuis. For lack of ornamental value, brocchinias tend to be missing from horticultural collections, thus complicating study of their physiology. While relatively confined geographically, *Brocchinia* has evolved a number of distinct habits and has radiated into a variety of terrestrial habitats and even moist forest canopies. No other pitcairnioid produces tank leaves (fig. 1) and only the occasional *Pitcairnia* roots with any frequency in tree crowns. Of all the brocchinias, *Brocchinia reducta* is probably among the most heavily dependent on leaves for mineral ion uptake. It usually roots in moist, infertile soil and produces tubular shoots partially filled with rainwater and insect remains. The following report describes analyses of *B. reducta* trichomes: implications of the findings to relationships among bromeliad subfamilies and to the evolution of epiphytism in Bromeliaceae are discussed.

MATERIALS AND METHODS

Brocchinia reducta specimens used in this study were growing on a damp-sand savanna near Km 148 along the El Dorado-Santa Elena Road in Estado Bolívar (5°48'N, 61°25'W) in the Gran Sabana region of southeastern Venezuela. Sections of tissue 4–5 cm square were excised from leaf bases and blades in the field, rinsed with deionized water and placed in plastic petri dishes. A buffered solution (pH 5.7) containing CaCl_2 and KH_2PO_4 (both 10^{-5} M) and ^3H -leucine at 10 $\mu\text{Ci/ml}$ (specific activity 17.5 mCi/mM) was pipetted onto a confined central area on air-dried foliar surfaces. After 0.5 hr, treatment solutions were removed with several deionized water rinses. Small squares of tissue were then excised from treated areas and immediately killed and fixed in FAA (formalin, acetic acid, ethanol). Two to three weeks later in Oberlin, tissues were dehydrated, embedded in Paraplast, sectioned at 8–10 μm , and mounted on glass slides. Following removal of the paraffin and rehydration, slides and tissue were coated with NTB-2 Kodak photographic emulsion, exposed for 8 days, and developed. Scanning electron micrographs were prepared using critical-point dried, gold-coated specimens and a Hitachi Model S-405A SEM operating at 25 kV accelerating voltage. Specimens stored in FAA were washed and refixed in 2% glutaraldehyde and 1% OsO_4 prior to critical-point drying. A voucher specimen of *B. reducta* (BEN

#101) is on deposit in the Oberlin College Herbarium, as are specimens of *Catopsis nutans* (BEN #102), *Tillandsia paucifolia* (syn. with *T. circinnata*; BEN #103), and *T. ionantha* (BEN #104); these were used to illustrate bromeliad trichomes. A second *B. reducta* voucher (BEN #101) is deposited at the Selby Botanical Gardens Herbarium (SEL). Other figures were duplicated from cited literature.

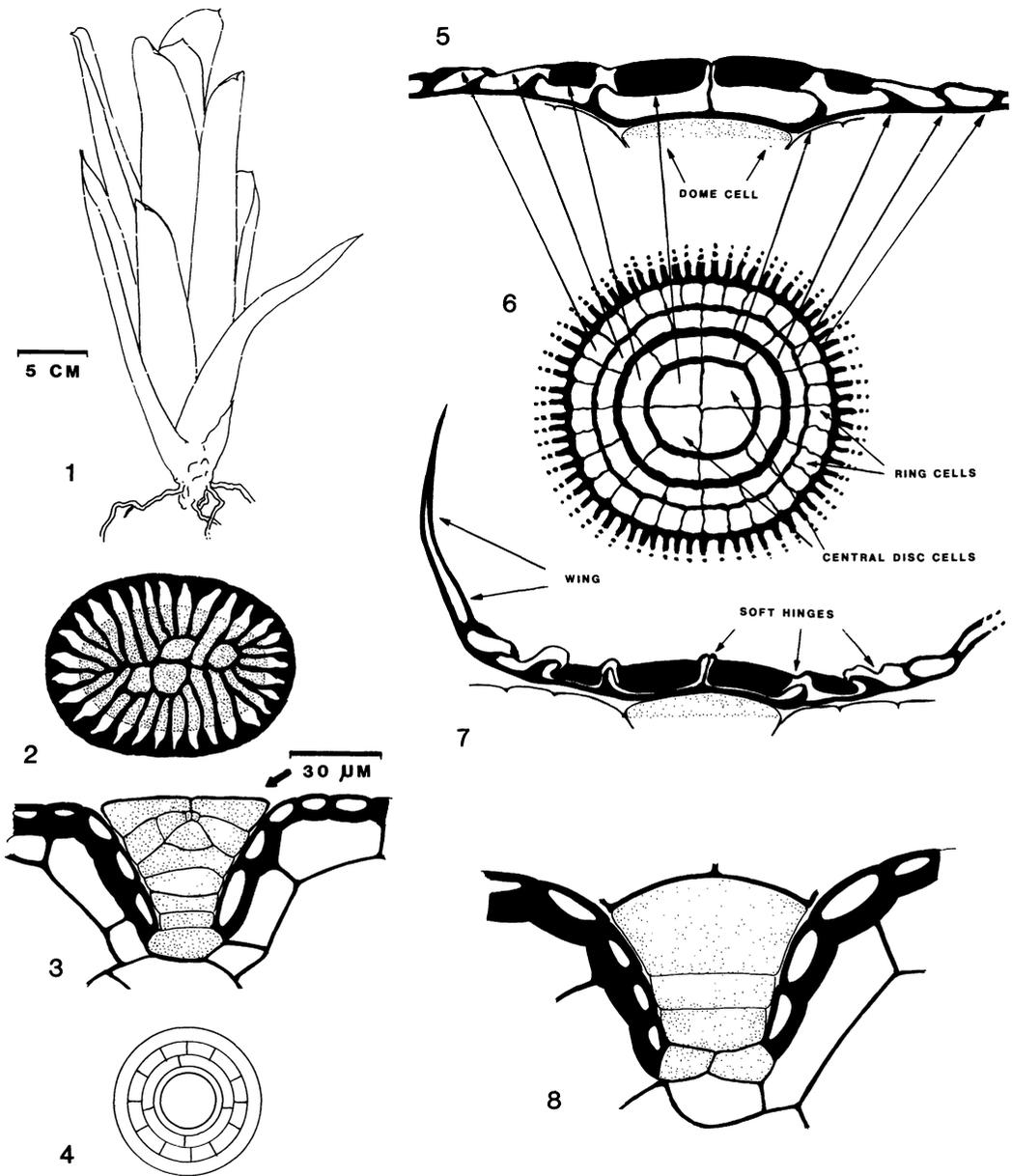
RESULTS

Foliar hairs of *Brocchinia reducta* differ from those of other adult bromeliads in at least two ways: all member cells remain alive after maturation and the stalk is multiseriate at its distal end (fig. 3). Partially concentric in arrangement (fig. 4), the trichome of *B. reducta* lacks the four upper tier disc cells that dominate the center of expanded, highly organized, tillandsioid trichome caps (figs. 2, 6, 13, 15, 23). In common with those of the most mesic, shade-tolerant members of Tillandsioideae, *B. reducta* trichomes do not extend beyond the epidermal concavity in which they are seated (figs. 18, 19, 21, 22). All cells of adaxial and abaxial trichome shields (caps) and stalks accumulated tritiated leucine (fig. 19). In contrast, trichomes well above the tanks exhibited no uptake and, in fact, were partially collapsed by the time collections were made (fig. 20).

DISCUSSION

Profiles of the subfamilies. The morphology of pitcairnioid flowers and fruits varies, ranging from fairly generalized in such genera as *Puya* and *Fosterella* to much more specialized in *Ayensua*, *Brocchinia*, and *Pitcairnia*. Seeds are naked or appendaged. Taxa of Pitcairnioideae exploit a wide continuum of substrata ranging from relatively equable to decidedly infertile and droughty. Pitcairnioids bear a variety of trichome forms. Hairs of most species are pelate and feature uniseriate stalks (figs. 11–12); other hairs lack caps (fig. 16; Robinson 1969; Tomlinson 1969). Root systems are usually well developed for absorption and anchorage. Herefore, no leaves have been found that bear obvious adaptations for solute or moisture uptake except for those of *Brocchinia*.

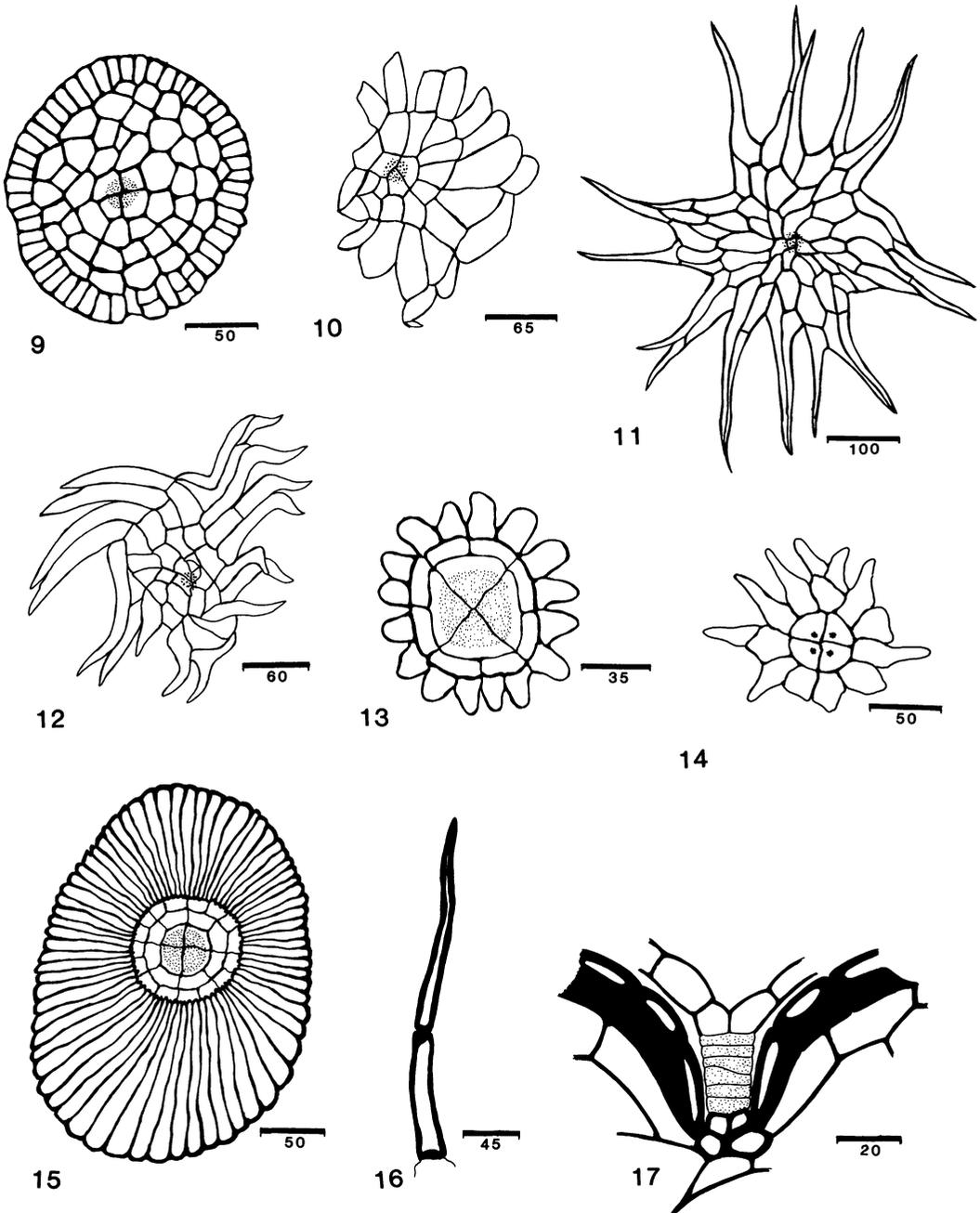
Many Bromelioideae occupy stressful habitats, a development associated with evolution of unusual habits and trichome specializations. Numerous bromelioid genera contain epi-



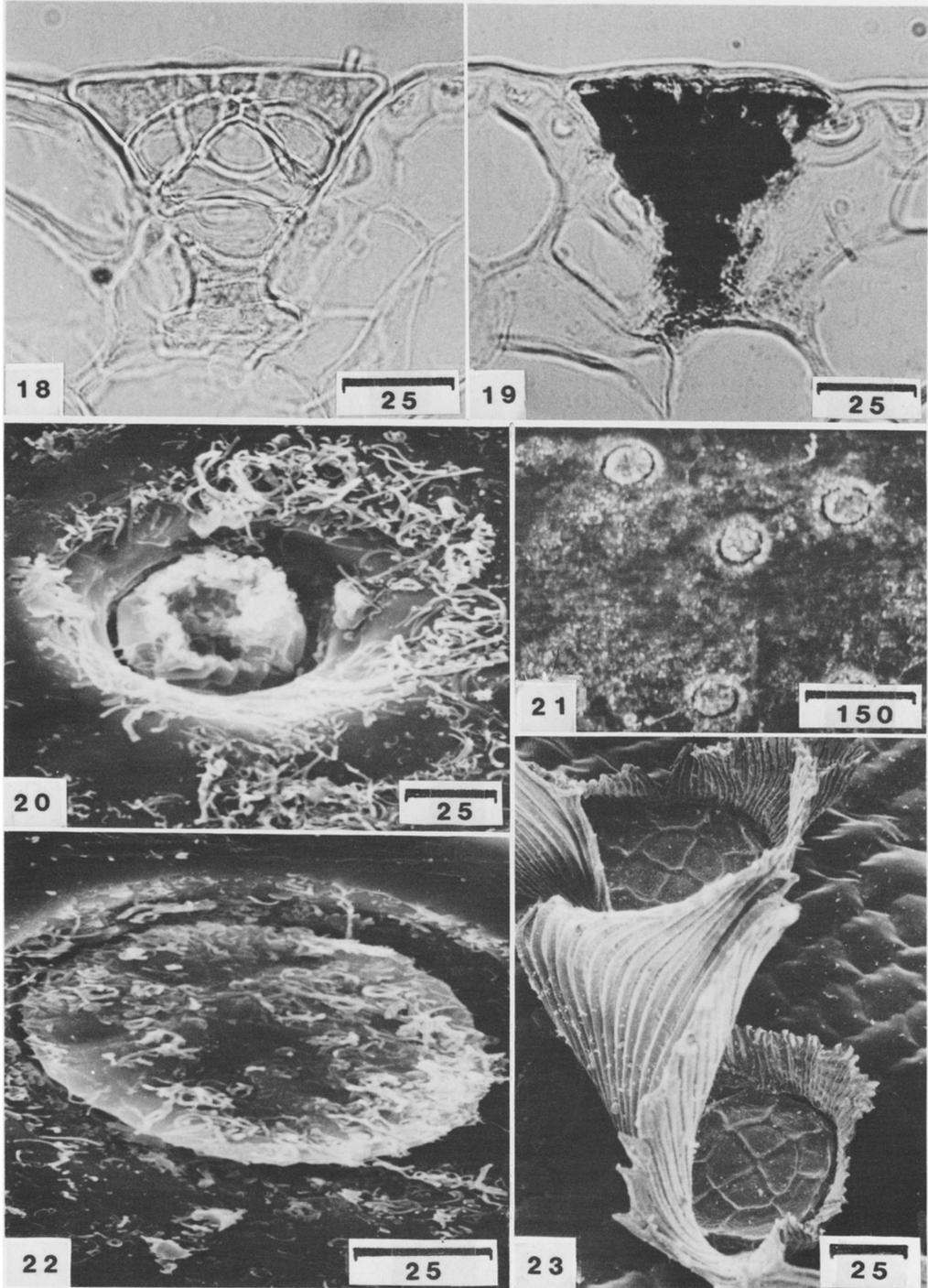
FIGS. 1-8. Aspects of bromeliad anatomy. Stalk regions of trichomes are stippled. 1. Habit of *Brocchinia reducta* (BEN #101). 2. Top view of *B. reducta* trichome cap. 3. Cross section of *B. reducta* trichome stalk. 4. Radial organization of *B. reducta* trichome cap. 5. Xeric *Tillandsia* trichome cap: hydrated configuration. 6. Top view of central region of xeric *Tillandsia* trichome stalk. 7. Xeric *Tillandsia* trichome cap: dehydrated configuration. 8. Cross section of xeric *Tillandsia* trichome stalk.

phytes, most of which are tank formers. Their expanded, tightly overlapping leaf bases, lined with peltate epidermal hairs that are absorptive in the species examined so far, entrap abundant

moisture and organic matter (Benzing et al. 1976; Sakai and Sanford 1980). All Bromelioideae possess essentially epigynous flowers and fleshy or leathery, indehiscent fruits.



FIGS. 9-17. Trichome structure of bromeliads and *Statice pruinosa*. Bars are in μm . 9. Cap of *Canistrum fosterianum* (from Tomlinson 1969). 10. Cap of *Navia serrulata* (from Robinson 1969). 11. Cap of *Fosterella penduliflora* (from Tomlinson 1969). 12. Cap of *Cottendorfia argentea* (from Robinson 1969). 13. Cap of *Catopsis nutans* (BEN #102). 14. Trichome of *Statice pruinosa* (from Lipshitz and Waisel 1982; magnification not given). 15. Cap of *Tillandsia paucifolia* (BEN #103). 16. Trichome of *Navia wardackii* (from Robinson 1969). 17. Stalk of *Canistrum fosterianum*.



FIGS. 18-23. Trichome structure of bromeliads. Bars are in μm . 18. Adaxial leaf base trichome of *Brocchinia reducta*: untreated control. 19. Adaxial leaf base trichome of *B. reducta* after treatment with ^3H -leucine. 20. Collapsed adaxial *B. reducta* trichome. 21. Intact adaxial leaf base trichomes of *B. reducta*. 22. Adaxial leaf base trichome of *B. reducta* showing loose cuticular filaments. 23. Abaxial trichome of atmospheric *Tillandsia ionantha* (BEN #104) showing soft hinges in uplift mode.

Tillandsioids usually root on bark or rock rather than in soil. A majority produce tanks. Peltate absorptive trichomes may densely cover the entire shoot, particularly in the case of the xeric, nonimpounding, largely rootless "atmospherics"—those species most specialized for moisture and mineral absorption in canopy habitats (Benzing and Renfrow 1980; figs. 5–8, 15, 23). While bearing less advanced flowers and fruits, tillandsioids feature wind-borne seeds with elaborate comas.

Glomeropitcairnia, a genus of just two tank tillandsioid species native to Venezuela and the southernmost Lesser Antilles, is of special interest to this discussion since its propagules, like those of *Brocchinia*, possess hairs at both ends. Moreover, *Glomeropitcairnia* ovaries are half-inferior while those of *Brocchinia* are half-to fully inferior. Flowers of other Tillandsioideae are fully hypogynous. Additionally, trichome stalks of *Glomeropitcairnia*, as well as those of certain brocchinias, contain more superposed cells than do those of most other pitcairnioids and all other tillandsioids. Stalk cell number can be as low as three—e.g., atmospheric *Tillandsia* (fig. 8; Tomlinson 1969). Reductions in the number of stalk cells have been thought to signal evolutionary advancement in Bromeliaceae (Harms 1930; Tomlinson 1969).

Trichome shield specialization. Shields of trichomes borne by atmospherics (figs. 5–7, 15, 23) are positioned closely enough to create a confluent, light-scattering indumentum that promotes water economy and provides protection from intense insolation in exposed, arid habitats (Benzing et al. 1978). Movements promoted by soft hinges, wall thickenings, and subjacent sculpturings in the central shield region (figs. 5–7) maximize stalk cell contact with passing canopy fluids. When shields are dry, the central disc collapses and wings flex upward, enhancing both water retention and light scattering (figs. 5–7; Mez 1904; Benzing et al. 1978; Benzing 1980, pp. 68–73; Benzing and Pridgeon 1983). Shields of mesic tillandsioids bearing narrower, less mobile margins (fig. 13) still participate in moisture and nutrient ion accumulation (Mez 1904; Benzing et al. 1976). Some bromelioids and other pitcairnioids in addition to *Brocchinia* also bear foliar hairs that show crude radial alignments of upper cells (figs. 2, 9–12; Benzing 1980). Flooding of associated leaf surfaces produces no shape changes

such as those noted when dry shields of atmospheric tillandsioids abruptly fill with water. *Brocchinia reducta*, tank bromelioids, and mesic tillandsioids provide proof that uptake function in bromeliad trichomes need not be accompanied by expanded, elaborately sculptured, mobile, concentric shields. Shield mobility associated with the most advanced tillandsioid trichomes is probably indispensable only if moisture and salts must be drawn exclusively from fluids whose contact with leaf surfaces is brief.

Theories on the ecological history of Bromeliaceae. Central to theories of bromeliad evolution is the modification of leaves to promote independence from soil. Pitcairnioideae has received little note because most pitcairnioid taxa are exclusively terrestrial. Pittendrigh (1948) proposed that Bromelioideae entered the epiphytic biotope by way of a soil-based ancestor resembling *Bromelia humilis* Jacq., a semi-succulent species native to impoverished, seasonally dry soil. This bromelioid exhibits rudimentary impoundments in which small amounts of debris and moisture are exploited by upward-growing roots and foliar trichomes. More advanced subfamily taxa owe their success in tree crowns to better-developed, rosulate, tank shoots (e.g., *Aechmea*, *Billbergia*). Pittendrigh (1948) also posited a xeric, soil-rooted prototype for Tillandsioideae on the grounds that primitive epiphytic tillandsioids were similar to modern atmospherics in lacking tanks; later, more mesomorphic forms emerged. Thin, impounding leaves appeared, bearing fewer, less complex (and functionally less important) leaf blade trichomes. Pittendrigh's scheme runs counter to another proposed earlier. Schimper (1888) postulated a mesic, pre-epiphytic, stock that dwelt in the forest understory before gaining access to lower branches; xeric, heliophilic epiphytes came later (fig. 24).

Pittendrigh's belief that mesomorphic, impounding forms such as *Guzmania lingulata* (L.) Mez and *Vriesea simplex* (Vell.) Beer remain basically heliophilic (a fundamental tenet of his theory) was challenged by findings that such species employ C3 carbon fixation and are efficient harvesters of weak light (Benzing and Renfrow 1971a, b; Benzing and Friedman 1981; Griffiths and Smith 1983). Values for $\delta^{13}\text{C}$ (Medina et al. 1977), nocturnal CO_2 uptake and acid rhythms (Coutinho 1965; McWilliams 1970;

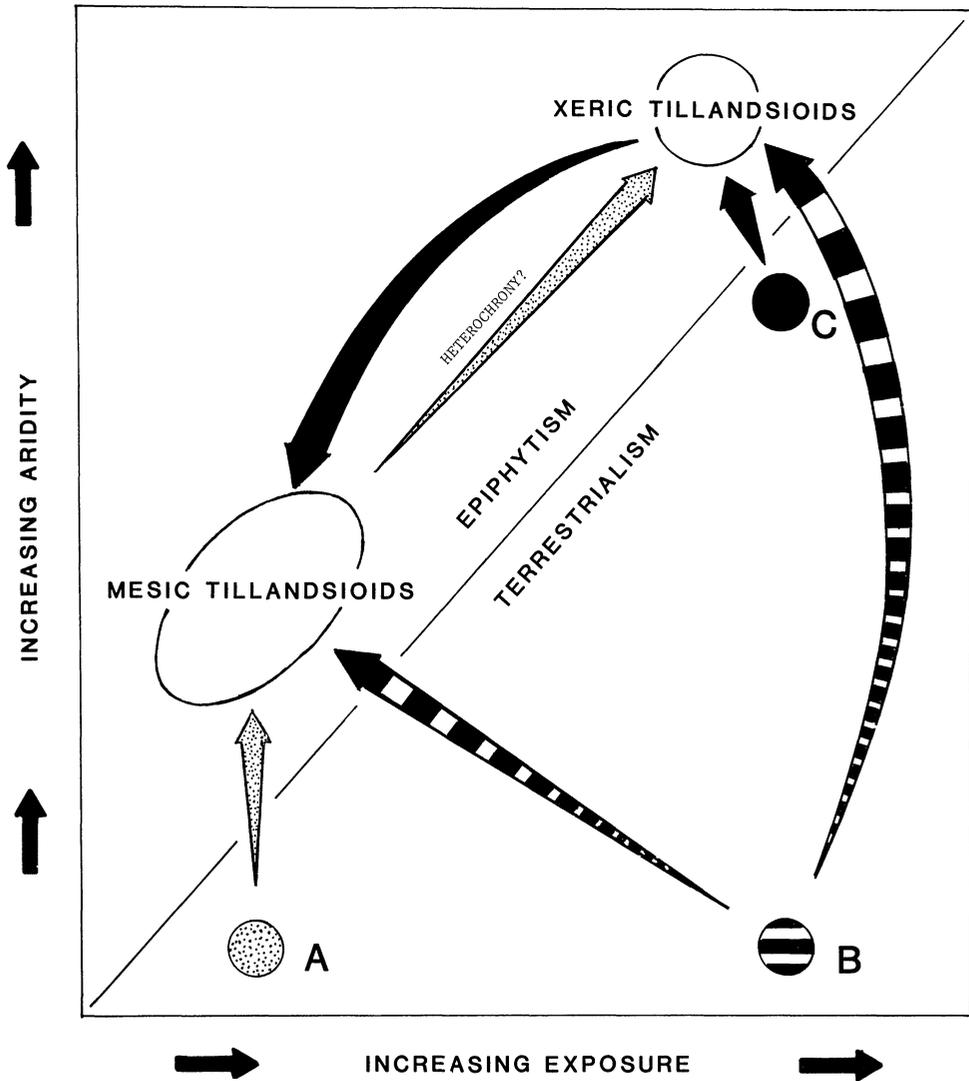


FIG. 24. A schema depicting three theories of tillandsioid evolution, each based on an ancestor adapted to dissimilar degrees of exposure and humidity. Schimper (1888): Common ancestor A via stippled arrows to mesic, thence to xeric, tillandsioids (perhaps via heterochrony; Tomlinson 1969; Benzing and Burt 1970). Medina (1974): Common ancestor B via broken arrows to both mesic and xeric tillandsioids. Pittendrigh (1948): Common ancestor C via solid arrows to xeric, thence to mesic, tillandsioids.

Medina 1974; Medina and Troughton 1974; Griffiths and Smith 1983), and leaf anatomy (Ortlieb and Winkler 1977) further indicate that thin-leaved, sparsely trichomed tillandsioids operate in the C₃ mode, and that more xeric, less shade-tolerant relatives with succulent shoots fix much of their CO₂ via CAM. The C₃ pathway is considered basic in taxa exhibiting

mixed photosynthetic strategies (Kluge and Ting 1978).

Pittendrigh's theory of a xeric ancestral home for Tillandsioideae seemed to draw support from the fact that the most primitive floral anatomy is found in *Tillandsia*, the genus containing the most xeric, heliophilic tillandsioids. Even if we grant that vegetative and re-

productive systems evolved synchronously, this proposal should be subjected to intense scrutiny. Within *Tillandsia*, both floral anatomy and degree of xerophytism vary. According to Smith (1934), subgenus *Allardtia* of *Tillandsia* possesses the least specialized flowers in the genus. However, many of its species utilize C3 photosynthesis, and have tanks and mesomorphic foliage with sparse trichome development. Only two of eight taxa tested exhibited CAM (Medina 1974). Recent findings confuse the search for the primitive tillandsioid habit still further. The basic floral structure of subgenus *Allardtia* also occurs among some very specialized atmospheric populations in other subgenera of *Tillandsia* and may be polyphyletic (Gardner 1982). Gilmartin (1983) has concluded from a cladistic analysis of the entire *Tillandsia/Vriesea* complex that xerophytism arose more than once in Tillandsioideae. She also proposed that these genera are basically mesic and noted that primitive members of *Tillandsia* subg. *Phytarrhiza* are tank-forming, cloud forest inhabitants that can tolerate low light intensities.

Medina (1974) adopted a third position vis-à-vis tillandsioid evolution, largely on the basis of photosynthetic behavior throughout the group and the habitat preferences of many South American Pitcairnioideae. He proposed that xeric and mesic lines very likely radiated into canopy habitats after diverging from a heliophilic C3 stock that was adapted to open sites on wet soils of the sort many pitcairnioids inhabit today (fig. 24). He also pointed out that exposure preferences of extant tillandsioids may not reflect those of precursors. We agree, but continue to believe, as implied earlier (Benzing and Renfrow 1971a), that analysis of the photosynthetic apparatus and leaf anatomy of xeric, heavily trichome-invested tillandsioids may reveal relictual qualities reflecting earlier accommodations to dim light and more profligate water use.

Medina (1974) also questioned a suggestion previously made by several authors (Schulz 1930; Tomlinson 1969; Benzing and Burt 1970) that atmospheric tillandsias and vrieseas are products of neoteny, their immediate antecedents having been native to wetter, darker habitats. Cited as evidence for heterochrony were outwardly similar qualities of trichome density, leaf succulence, and habit between the young of tank forms and the seedlings and

adults of related atmospheric. Medina theorized that these anatomical peculiarities of tank juveniles could be explained just as well by recapitulation of ancient xeric traits. A demonstration that seedlings of many modern tank-forming tillandsioids are indeed more similar to atmospheric relatives than to their own later growth stages in certain aspects of epidermis and habit would help resolve this question. Seedling physiology also should be examined to determine whether a period of complementary CAM activity accompanies what appears to be transient xeromorphy. The neotenic argument as applied to tillandsioid evolution is most appealing if based on the premise that selective pressures impinging on tank seedlings and atmospheric are much alike, and shared juvenile characters are adaptive for the same reasons in both cases. If Medina's biogenetic alternative is right, these traits, when present in seedlings of tank species, would either complement processes other than water and carbon balance or be vestigial—i.e., non-functional.

Medina's (1974) belief that juveniles and adults of soft-leaved impounding taxa are not likely to differ in moisture requirement because they share the same mesic habitats presumes that both are equally resistant to desiccation and acquire and use water in the same fashion. This is not necessarily so. Small-size seedlings tend to have less favorable surface-to-volume ratios than have adults, thus less capacity for moisture retention. Moreover, tank tillandsioid seedlings remain tankless for several years (pers. obs.); without access to impounded fluids, they experience stronger drought selection than do more mature specimens. Even very brief rainless episodes must challenge small plants anchored on shallow, relatively non-porous bark with no auxiliary source of moisture.

If the early tillandsioids were tank formers whose juveniles were comparable to those of modern counterparts, they could have been ancestral to xeric atmospheric. Heterochrony may well have been the vehicle needed to exploit that potential, allowing primitive Tillandsioideae to penetrate the drier parts of the forest canopy where tanks cannot provide a reliable moisture supply. Unquestionably, absorbing trichomes would have facilitated this evolutionary advancement. Medina (1974) made no

specific comments about trichome evolution. Pittendrigh (1948) stated that he could see no reason why an absorbing hair would arise where it provided no benefit (under mesic circumstances). The answer may lie in precedents in other taxa equipped with foliar impoundments, and a fuller recognition that bromeliad trichomes are involved in nutrient as well as moisture uptake.

Evolutionary implications. The discovery that absorbing trichomes are borne by one or more species in every subfamily of Bromeliaceae mandates revision of certain concepts of bromeliad evolution. We must now accept the possibility that the family prototype was already capable of using its shoots to obtain nutrients and moisture. Examination of other vegetative features further suggests that Tillandsioideae and Pitcairnioideae (by way of *Broccchinia*) bear more resemblance to one another than either does to Bromelioideae. So far, all bromelioids have proved to be CAM plants (McWilliams 1970; Medina and Troughton 1974; Bartholomew 1982; Griffiths and Smith 1983), a feature consistent with Pittendrigh's view of the subfamily's ancestry. A few are impounding terrestrials and epiphytes adapted to deep shade (e.g., some species of *Nidularium* with thin, discolorous leaves; Benzing and Friedman 1981). Others without tanks are native to near-aquatic conditions in wet soil (e.g., several *Cryptanthus* spp.; E. Medina pers. comm.). Here, CAM is weak and appears to be relictual or at least represents an unexpected feature in shoots that otherwise are well designed to harvest filtered light deep in dense forests. Presumably, nocturnal CO₂ fixation in these taxa is a holdover from times when high water use efficiency was more crucial to survival.

Pitcairnioideae and Tillandsioideae share a tank habit that is more mesic than that of Bromelioideae. Medina et al. (1977) demonstrated that tank-forming, mesomorphic *Broccchinia acuminata* L. B. Smith, *B. micrantha* (Baker) Mez, *B. reducta*, and *B. tatei* L. B. Smith are all C3 species. Tank habits and epiphytism are associated in all three subfamilies of Bromeliaceae. *Broccchinia acuminata* is occasionally epiphytic while *B. tatei* is commonly found in tree crowns along the El Dorado-Santa Elena Road as one ascends the Escalara to the Gran Sabana. *Broccchinia tatei* is particularly noteworthy for its remarkable similarity in leaf texture, habit, and

occurrence in wet forests to hundreds of mesic species representing every tillandsioid genus. Thick layers of loose, white, cuticular wax (fig. 22) cover the leaves, particularly the bases, of *B. tatei* and *B. reducta*, as well as those of several species in *Catopsis* and *Tillandsia* (both Tillandsioideae).

The *B. reducta* system (habitat preference, nutrition, and foliar hairs) suggests that at least some bromeliad trichomes have acquired absorptive capacities in the absence of strong drought selection. Given the impoverished but well-watered substrata supporting this pitcairnioid and its numerous animal-trapping associates (e.g., the South American pitcher plant, *Heliamphora*), the impetus for deployment of tank leaves bearing absorbing hairs appears more closely tied to nutrient than to moisture procurement. This suggestion is consistent with another notion: that impounding shoots arose in *Broccchinia* to promote carnivory (McWilliams 1974). We need not look very far for comparable precedents elsewhere. Foliar impoundments and associated absorptive trichomes serve plants in several other families native to moist, exposed, infertile habitats (e.g., Cephalotaccaceae, Nepenthaceae, Sarraceniaceae). In many cases, trap-associated hairs are glandular, processing prey as well as subsequently taking up released nutrients. Similar duality has not been reported in a bromeliad, but Picado (1913) did record digestive enzymes in the impoundment fluids of some Costa Rican tillandsioids, a discovery that requires confirmation under much stricter controls. The unusual acidic character (pH approx. 3.0) of *B. reducta* tank fluids (pers. obs.) also is worthy of comment: perhaps the pH is lowered by adjacent leaf tissue, possibly in conjunction with uptake of certain organic solutes as part of a hydrogen ion/amino acid co-transport system, or an acid-activated carrier complex such as that associated with glands lining *Dionaea muscipula* traps (Rea and Whately 1983). Regardless of why *B. reducta* trichomes were originally modified for nutrient uptake, this species certainly has access to abundant animal tissue as a major source of organic nitrogen and mineral ions. Most of the solid matter in tanks of *B. reducta* consists of drowned ants (Givnish et al. 1984).

In view of information currently at hand, the most parsimonious hypothesis for the evolution of absorptive trichomes in Pitcairnioideae

would cast the foliar hair of *B. reducta* as an adjunct to the tank habit, not as a high-speed, nutrient-garnering device to aid a tankless ancestor gain nourishment from passing precipitation (as Pittendrigh suggested was true for Tillandsioideae). Since there is as yet no evidence for absorbing trichomes in non-impounding pitcairnioids, the absorptive capacity of the *Brocchinia* trichome is best viewed as a mechanism that evolved to acquire nutrients released from impounded animal prey or degrading vegetable debris in the fashion of extant tank bromelioids and tillandsioids. Early tillandsioids may have followed a similar adaptive sequence, or they and an equally ancient *Brocchinia* relative could have inherited common trichome qualities and habit from a single ancestor. In either instance, shield elaborations came later as tillandsioid trichomes evolved the capacity to absorb moisture and solutes without benefit of long-term contact with tank fluids. Similar elaborations apparently have not developed in Pitcairnioideae. Convergence, of course, remains a plausible alternative. The bromeliad trichome design is not unique; many other lineages have evolved foliar hairs capable of solute exchange. At least one, the salt-excreting appendage of halophytic *Statice* (Plumbaginaceae), is remarkably similar in structure to that of Tillandsioideae (fig. 14; Lipschitz and Waisel 1982). Whether convergence or parallelism explains their similarities, Pitcairnioideae and Tillandsioideae appear to be more closely related than previously thought.

Brocchinia and tillandsioid genera, especially *Glomeropitcairnia*, should be compared for evidence of close evolutionary relationship, with foliar hairs as a major focal point. Those borne by various pitcairnioids, particularly brocchinias lacking well-developed tanks, must be examined more closely for attributes that promote fitness and for similarities with comparable tillandsioid appendages. Attempts to use characters of major ecological import in studies of bromeliad evolution should continue. Adaptive radiation throughout Bromeliaceae was accompanied by major changes related to problems of resource acquisition in diverse and often very stressful environments. This family provides an unusual opportunity for functional analysis as well as for more traditional meth-

odologies designed to reveal adaptive and ecological aspects of its phylogeny.

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