PETAL APPENDAGES IN BROMELIACEAE¹

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The Bromeliaceae were surveyed for petal appendage morphology using light and scanning electron microscopy. Three general morphological types were recognized, each loosely correlating with one of the three subfamilies. Petal appendage elaboration and variation were greatest in the Bromelioideae, while subfamilies Pitcairnioideae and Tillandsioideae exhibit more simplified, consistent morphologies. All Pitcairnioideae examined with petal appendages possessed a single appendage per petal, as opposed to two appendages per petal for the Bromelioideae and Tillandsioideae. Analyses of floral ontogenetic sequences revealed that, in all cases, petal appendage initiation is a late developmental event with petal appendages being the last formed external multicellular structures. There has been an overemphasis in the use of the presence of petal appendages in the circumscription of generic limits in the Bromeliaceae, and especially in the Tillandsioideae (e.g., *Tillandsia* vs. *Vriesea*).

Approximately 35% of the over 2,100 species in the Bromeliaceae (sensu Smith and Downs, 1974, 1977, 1979) are known to have petal appendages. These appendages are outgrowths from the adaxial surface of the petal, usually at its base. They consist of a single flap of tissue between the antipetalous staminal filament and the petal (e.g., Fig. 36), or as a pair of structures that flank each antipetalous stamen (e.g., Figs. 7 or 45). Names applied to bromeliad petal appendages include: petal scales, ligules, nectariferous scales, lateral folds, vertical calli, and callosities.

Petal appendages have received great emphasis in Bromeliaceae taxonomy. In the introduction to their monograph for the family, Smith and Downs (1974) state that petal appendages are the single most important taxonomic character for the subfamilies Bromelioideae and Tillandsioideae. In fact, petal appendages have diagnostic utility at the generic level in all three bromeliad subfamilies (Smith and Downs, 1974, 1977, 1979; Table 1). However, many current students of the family, for example, Beaman (1989), Benzing (1980; personal communication), K. Burt-Utley (University of New Orleans, personal communication), S. Gardner (Michoacan, Mexico, personal communication), Gilmartin (1983; personal communication), H. Luther (Selby Botanical Gardens, personal communication), C. Palaci (University of Wyoming, personal communication), Rauh (1979; personal communication), and Utley (1978; personal communication) are skeptical of certain generic circumscriptions that rely heavily on the presence or absence of petal appendages.

Particularly controversial is the use of petal appendages

to circumscribe genera in Tillandsioideae. The first and third largest genera in Bromeliaceae, *Tillandsia* (400+ spp.) and *Vriesea* (250+ spp.), are separated on the basis of absence or presence of petal appendages, respectively. Benzing (1980) has called this "... perhaps the most arbitrary taxonomic decision standing in the Tillandsioideae today." Utley (1978) also questioned the soundness of separating genera on the basis of presence or absence of petal appendages, and noted the need to reexamine generic boundaries in the Tillandsioideae. Gilmartin (1983) considered it unlikely that the petal appendages used to separate *Vriesea* from *Tillandsia* are uniquely derived. Beaman (1989) stressed the need to evaluate the single character (i.e., petal scales) used to distinguish *Tillandsia* and *Vriesea*.

Baker (1889) treated *Vriesea* as a subgenus in *Tillandsia* to accommodate those species where the "claw of the petals (are) furnished with a pair of scales. . . ." Mez (1904, 1934–1935) followed Baker (1889) in the separation of *Tillandsia* and *Vriesea* on the basis of petal appendages when he elevated *Vriesea* to generic status. After many years of bromeliad research, Smith (1951) applied his current concept of the *Tillandsia*-*Vriesea* distinction when transferring all species of *Tillandsia* with petal appendages into *Vriesea*, and he has maintained these generic circumscriptions since that time (e.g., Smith and Downs, 1977).

A review of *Tillandsia* and *Vriesea* nomenclatural history reveals cases where a species was first described in one genus (e.g., *Tillandsia rubra* Ruiz Lopez & Pavón; *T. ingens* Mez) and later had to be transferred to the other (e.g., *Vriesea*) when more complete material revealed the presence of petal appendages. Conversely, Smith and Downs (1977) chose to ignore the petal appendage character when they placed *Tillandsia pabstiana* Pereira (which lacks petal appendages) into synonymy under *Vriesea drepanocarpa* (Baker) Mez (which has petal appendages) because of the noted overall similarity between the two taxa. Furthermore, there are reports where petal appendage occurrence in *Vriesea* is sometimes variable (Read, 1968). The overall picture that has emerged, especially in the Tillandsioideae, is that petal appendages by themselves may not be a reliable generic marker.

Petal appendages are reported for 14 of the 27 genera in subfamily Bromelioideae (Table 1), and in three cases they serve as the critical diagnostic feature for generic

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TABLE 1. Frequency of occurrence of petal appendages in Bromeliaceae genera with petal appendages; (number of species in the genus with petal appendages/total number of species in the genus)

Bromelioideae	
<i>Acanthostachys</i> (2/2)	<i>Hohenbergia</i> (40/40)
<i>Aechmea</i> (168/172)	<i>Neoglaziovia</i> (2/2)
<i>Ananas</i> (8/8)	<i>Nidularium</i> (1/23)
<i>Billbergia</i> (53/53)	<i>Orthophytum</i> (17/17)
<i>Canistrum</i> (7/7)	<i>Portea</i> (7/7)
<i>Fascicularia</i> (5/5)	<i>Quesnelia</i> (14/14)
<i>Greigia</i> (1/26)	<i>Wittrockia</i> (7/7)
Pitcairnioideae	
<i>Abromeitiella</i> (2/2)	<i>Pitcairnia</i> (134/260)
<i>Brewcaria</i> (2/2)	<i>Puya</i> (6/168)
<i>Deuterocohnia</i> (7/7)	<i>Steyerbromelia</i> (3/3)
Tillandsioideae	
<i>Glomeropitcairnia</i> (2/2)	<i>Mezobromelia</i> (4/4)
<i>Vriesea</i> (249/249)	

recognition (Table 2). As with the Tillandsioideae, Smith and Downs (1979) placed substantial weight on petal appendages for their taxonomy of the Bromelioideae. In contrast, however, issues surrounding the taxonomic implications of petal appendages in the Bromelioideae have been debated less perhaps because the generic delineations in the Bromelioideae are "... so poorly defined that even with complete information it is difficult to assign some species to genus" (Smith and Downs, 1979). Clarifying generic circumscriptions and phylogenetic relationships within the Bromelioideae will be a formidable task. Efforts to revise parts of Bromelioideae are currently under way. For example, I. Ramirez (Epiphyte Symposium, Selby Botanical Gardens, Sarasota, FL, 1991) has reported that petal appendages are synapomorphic for *Neoregelia* subg. *Hylaeicum*.

The taxonomic utility and importance of petal appendages have been less in the Pitcairnioideae. Six of the 15 genera have petal appendages (Table 1), but they help define only *Abromeitiella*, *Deuterocohnia*, *Brewcaria*, and *Steyerbromelia*. In *Pitcairnia* and *Puya*, the two largest genera in the subfamily, petal appendages are variable in their occurrence, being characteristic for certain species. Petal appendage occurrence is also variable within certain species of *Pitcairnia* and *Puya* (e.g., *Pitcairnia pulverulenta* Ruiz Lopez & Pavón; *P. schultzei* Harms; *Puya hofstenii* Mez; Varadarajan, 1986; Varadarajan and Brown, 1988).

The goals of this study were to: 1) conduct a broad survey of petal appendage morphology within the Bro-

melioideae; 2) examine petal appendage ontogeny in each subfamily; and 3) utilize the information collected to address issues concerning the systematic value of petal appendages within Bromeliaceae, especially in the Tillandsioideae.

MATERIALS AND METHODS

All floral materials were obtained from field or greenhouse collections that had been preserved in FAA (formaldehyde : glacial acetic acid : absolute ethanol; 1:1:18; v:v:v) or Farmer's fixative. Field-collected samples were obtained mostly through the efforts of a network of field collaborators (Gilmartin and Brown, 1986). Cultivated materials were obtained from either: 1) Selby Botanical Gardens, Sarasota, Florida; 2) Botanical Garden, Institute for Systematic Botany, University of Heidelberg, Heidelberg, Germany; 3) Denver Botanical Gardens, Denver, Colorado; or 4) the botany greenhouse, University of Wyoming, Laramie, Wyoming. The intergeneric hybrids employed in this study ($\times$ *Cryptbergia* = *Cryptanthus* $\times$ *Billbergia*; $\times$ *Vrieslandsia* = *Vriesea* $\times$ *Tillandsia*) are of horticultural origin, and are commercially available. The sources for all plant materials and the locations for all herbarium vouchers are provided in Table 3.

After a minimum of 24 hr of fixation, floral collections were transferred into 70% ethanol and stored below 0 C. Dissections and initial examinations of petal appendage structure were made with a dissecting microscope.

Floral tissues destined for scanning electron microscopy required a special postfixation treatment to avoid deformation during critical-point drying (Brown and Gilmartin, 1989). After critical-point drying, specimens were mounted onto (SEM) stubs and sputter-coated with gold, examined with a JEOL JSM-35C SEM, and photographed with Polaroid type 665 film.

For the developmental studies, inflorescences were selected that had one basal flower in full anthesis and a complement of developing floral buds above. The entire inflorescence, or an inflorescence branch, was liquid preserved as described above. Individual flowers and buds were removed and assigned a number, and bud length (base of calyx to tip of calyx or tip of corolla, if exerted) was measured to the nearest mm. Bud/flower age was assigned relative to its position on the inflorescence or inflorescence branch. The smallest (i.e., the youngest) bud was assigned an "age" of 1, the bud on the next node down was designated "age" 2, etc., with the anthesis-stage flower receiving the oldest (i.e., highest age value). Each bud/flower of a developmental sequence was kept separate, i.e., in its own vial during all steps of dissection and tissue preparation. During bud dissections, anthers were removed and squashed under a coverslip in acetic carmine to determine the developmental status of the microspores or microspores.

The nomenclature, generic circumscriptions, and estimates of taxon numbers used here follow Smith and Downs (1974, 1977, 1979).

RESULTS

There are three general morphological syndromes for petal appendages in the Bromeliaceae, each correlating,

TABLE 2. Pairs of genera in the Bromeliaceae where the presence of petal appendages is a critical diagnostic feature

With petal appendages	Without petal appendages
Bromelioideae	
<i>Canistrum</i>	<i>Nidularium</i>
<i>Hohenbergia</i>	<i>Hohenbergiopsis</i>
<i>Portea</i>	<i>Neoregelia</i>
Tillandsioideae	
<i>Mezobromelia</i>	<i>Guzmania</i>
<i>Vriesea</i>	<i>Tillandsia</i>

TABLE 3. *Bromeliaceae* taxa illustrated in text

Taxon	Voucher
<i>Abromeitiella lorentziana</i> (Mez) Castell.	Palaci 775 (WS)
<i>Acanthostachys strobilacea</i> (Schultes f.) Klotzsch	SEL 81-169
<i>Aechmea araneosa</i> Lyman B. Smith	Martinelli 11619 (WS)
<i>A. caesia</i> E. Morren ex Baker	SEL 86-293
<i>A. chantinii</i> (Carriere) Baker	HEID s.n.
<i>A. contracta</i> (Martius ex Schultes f.) Baker	SEL 75-13-12
<i>A. distichantha</i> Lemaire	Palaci 624 (WS)
<i>A. distichantha</i> Lemaire	Brunner 1378 (WS)
<i>A. filicaulis</i> (Griseb.) Mez	SEL 75-90-74
<i>A. fulgens</i> Brongn. var. <i>discolor</i> (C. Morren) Brongn. ex Baker	SEL 87-458
<i>A. lasserii</i> Lyman B. Smith	DB 78968
<i>A. macvaughii</i> Lyman B. Smith	SEL s.n.
<i>A. nudicaulis</i> (L.) Griseb.	SEL 85-717
<i>A. nudicaulis</i> var. <i>nudicaulis</i>	Martinelli 11775 (WS)
<i>A. paniculigera</i> (Sw.) Griseb.	HEID 19897A
<i>A. serrata</i> (L.) Mez	SEL 86-292
<i>A. seideliana</i> Weber	DB 80564
<i>Ananas ananassoides</i> (Baker) Lyman B. Smith	Brunner 1488 (WS)
<i>Araeococcus flagellifolius</i> Harms	SEL 78-683
<i>Billbergia morelii</i> Brongn.	DB s.n.
<i>B. pyramidalis</i> (Sims) Lindley	Martinelli 11647 (WS)
<i>Billbergia</i> sp.	SEL s.n.
<i>Deuterocohnia meziana</i> O. Kuntze ex Mez	SEL 86-738
<i>Fascicularia bicolor</i> (Ruíz Lopez & Pavón) Mez	Flores 112 (WS)
<i>Hohenbergia correia-arauji</i> Pereira & Moutinho	DB 870460
<i>Mezobromelia bicolor</i> Lyman B. Smith	SEL 86-709
<i>M. bicolor</i>	Benzing s.n.
<i>M. fulgens</i> Lyman B. Smith	Madison et al. 7416
<i>M. lyman-smithii</i> Rauh & Barthlott	Gilmartin & Betancourt 3021 (WS)
<i>Orthophytum fosterianum</i> Lyman B. Smith	SEL 89-612
<i>O. leprosum</i> (Mez) Mez	SEL 82-437
<i>Pitcairnia lanuginosa</i> Ruíz Lopez & Pavón	SEL 82-543
<i>P. pulverulenta</i> Ruíz Lopez & Pavón	DB 79782
<i>P. punicea</i> Schweidweiler	SEL 80-1590
<i>P. xanthocalyx</i> Martius	Gilmartin 3175 (WS)
<i>Pitcairnia</i> sp.	Gilmartin & Betancourt 3107 (WS)
<i>Pseudananas sagenarius</i> (Arruda) Camargo	Brunner 1280 (WS)
<i>Quesnelia lateralis</i> Wawra	Martinelli 11571 (WS)
<i>Streptocalyx floribundus</i> (Martius ex Schultes f.) Mez	DB 78766
<i>Vriesea arpocalyx</i> (André) Lyman B. Smith	Betancourt 301 (WS)
<i>V. atra</i> Mez	Martinelli 10711 (WS)
<i>V. atro-purpurea</i> Silveira	Martinelli 10637 (WS)
<i>V. carinata</i> Wawra	Hatschbach 46-829 (WS)
<i>V. cereicola</i> (Mez) Lyman B. Smith	Vega 3866 (WS)
<i>V. ensiformis</i> (Vell. Conc.) Beer	Martinelli 9553 (WS)
<i>V. friburgensis</i> Mez	Gilmartin 3083 (WS)
<i>V. geniculata</i> (Wawra) Wawra	Hatschbach 47114 (WS)
<i>V. gladioliflora</i> (Wendl.) Antoine	DB s.n.
<i>V. gladioliflora</i>	SEL 78-1264
<i>V. glutinosa</i> Lindley	SEL 86-303
<i>V. graminifolia</i> Mez & Werckle	SEL 85-273
<i>V. incurvata</i> Gaudich.	Hatschbach 46-827
<i>V. malzinei</i> E. Morren	SEL 79-1780
<i>V. maxoniana</i> (Lyman B. Smith) Lyman B. Smith	Palaci 752 (WS)

TABLE 3. *Continued*

Taxon	Voucher
<i>V. neoglutinosa</i> Mez	Martinelli 11683 (WS)
<i>V. ospinae</i> Luther	SEL 80-754
<i>V. psittacina</i> (Hooker) Lindley var. <i>rubro-bracteata</i> Hooker	Martinelli 10633 (WS)
<i>V. recurvata</i> Gaudich.	DB 76-1555
<i>V. schwackeana</i> Mez	SEL s.n. ex hort
<i>V. simplex</i> (Vell. Conc.) Beer	Martinelli 11615 (WS)
<i>V. viridiflora</i> (Regel) Wittm. ex Mez	SEL 81-1905
<i>Vriesea</i> sp.	SEL 85-1363
<i>Vriesea</i> sp.	Martinelli 10921 (WS)
<i>Wittrockia</i> sp.	Martinelli 9743 (WS)
× <i>Cryptbergia</i> 'Mead'	Pineapple Place, Longwood, FL (RM)
× <i>Vrieslandisa</i>	Pineapple Place, Longwood, FL (RM)

more or less, with one subfamily. Bromelioideae, which are epigynous, have the most complex, derived floral structure in the family. It also exhibits the most complex and variable petal appendage morphology (Figs. 1–30). Pitcairnioideae are characterized by a relatively simple, solitary tongue-like petal appendage (Figs. 31–38). Tillandsioideae petal appendages come in pairs, as in Bromelioideae; however, they are all tongue-like in structure (Figs. 39–64).

Bromelioideae—When petal appendages are present, there are six per flower (i.e., two per petal), and these flank the antipetalous staminal filament. Attachment of appendages can be at (e.g., Figs. 2–6, 8–14) or just above the base (e.g., Figs. 1, 7) of the petal or point of hypanthium insertion. In some Bromelioideae the appendages are inserted relatively high on the adaxial surface of the petal or hypanthium (e.g., Figs. 19, 20, 23–25). The individual appendage can range from a small conspicuous bump (Figs. 16, 26; = callosities of some authors), to simple and tongue-like (Figs. 7–9, 15, 22), to pouch or sac-like (Figs. 2, 10, 13, 14, 18, 20, 21), to ornately fringed and tongue- or sac-like (Figs. 3–6, 11, 12, 19, 23, 27), to irregular masses (Figs. 24, 25), to longitudinal folds or ridges of various complexity (Figs. 17, 28–30). Sac- or pouch-like forms frequently display additional fringe elaboration or lobe production (Figs. 1, 13, 14, 18, 20). Figures 1–30 appear to represent the known range of petal appendage variation in the Bromelioideae. One addition to this range of variation may be *Aechmea bracteata* (Sw.) Griseb., where immature floral material indicates that each petal will likely have a single tongue-like appendage, as is characteristic for the Pitcairnioideae. It should be noted, however, that *A. bracteata* is autogamous and anomalous in other aspects of floral morphology (i.e., distinctive stigma type; Gortan, 1991; Brown, unpublished data). For the most part, bromelioid petal appendages are readily visible, although the smaller longitudinal fold or bumplike appendages are relatively cryptic.

Pitcairnioideae—The petal appendage consists of a single blade or tongue-like outgrowth from the petal base. The continuity of the appendage blade is evident from early development on to maturity (compare Figs. 31 and 32). The margin of the appendage blade is usually entire

Figs. 1-6. Bromelioideae petal appendages. Bars = 1.0 mm. 1. *Acanthostachys strobilacea*. 2. *Aechmea araneosa*. 3. *A. caesia*. 4. *A. chantinii*. 5. *A. contracta*, mature. 6. *A. contracta*, early development, postmicrosporogenesis anther.

Figs. 7-14. Bromelioideae petal appendages. Bars = 1.0 mm. 7. *Aechmea distichantha* (Palaci 624). 8. *A. distichantha* (Brunner 1378). 9. *A. fulgens* var. *discolor*. 10. *A. lasserii*. 11. *A. macvaughii*. 12. *A. nudicaulis* (SEL 85-717). 13. *A. paniculigera*. 14. *A. serrata*.

and bifid, or notched, at the apex (Figs. 34–36, 38), although there may be some distal teeth (Figs. 33, 37) or a fringe (Fig. 31). When petal appendages are present in pitcairnioid taxa, they are typically large and conspicuous. Several additional examples of petal appendage diversity in Pitcairnioideae are illustrated in Varadarajan and Brown (1988).

Tillandsioideae—Variability in tillandsioid petal appendages occurs mostly in the size and shape of the tongue-like blade, the nature of its margin, and surface ornamentation (e.g., Figs. 47, 51, 63). Petal appendages in Tillandsioideae are typically large and conspicuous. Exceptions are found in some species of *Vriesea* (e.g., Figs. 44, 48, 50) where appendages are small and obscure. Figures 39–64 represent the range of petal appendage variation known in *Mezobromelia* and *Vriesea*. *Glomeropitcairnia* also has petal appendages; however, none were available for this study.

Developmental studies—Petal appendage development was examined in several species from each subfamily. Some features of the process are consistent for the family. Petal appendage primordia (Figs. 65, 79, 85) appear late in development, just prior to the bud expansion phase preceding anthesis (Fig. 99). The initial appearance of petal appendage primordia may coincide with the start of microsporogenesis, although in most cases it coincides with the postmeiotic tetrad stage. Using Tucker's terminology (1988), the petal appendage primordia form during the start of the "late expansion, cell differentiation" phase. When petal appendages are present, they are the last external, multicellular structure to be formed in the flower.

In all subfamilies, the petal appendage primordia first appear on the adaxial petal surface as two small, frequently crescent-shaped, bumps that flank the antipetalous staminal filament (Figs. 65, 79, 85). In Bromelioideae (e.g., Figs. 66–78) and Tillandsioideae (Figs. 85–88) the primordia and developing appendages remain separate, while in the Pitcairnioideae the appendage primordia become united soon after initiation (Figs. 80, 81), and subsequent growth and development result in a single appendage positioned between the petal and opposing stamen (e.g., Figs. 79–84).

While traditionally recognized as petal appendages, the lateral folds (e.g., Fig. 17) found in some species may have a different ontogeny. These lateral folds have a pleated appearance, and may be the result of petal claw folding

due to physical constrictions placed on the corolla by the calyx. More work is needed to fully characterize these types.

Aechmea filicaulis was selected as representative for petal appendage development in the Bromelioideae. The mature petal appendage in *Aechmea filicaulis* (Fig. 78) is an elongated pouch- or sac-like structure that has varying degrees of irregular-toothing or elongated-lobing associated with the distal margin of the pouch. The pouch is attached to a long, ridgelike thickening of the adaxial petal surface, that among bromelioids usually extends distally along the petal to the level of the calyx apex, and partially encases the staminal filaments. Figures 28 and 96 illustrate this ridge in related taxa. Margins of the ridge adjacent to the antipetalous stamen many have irregular hornlike projections as in *A. filicaulis* (Figs. 77, 78).

The petal appendage primordia appear in *Aechmea filicaulis* in typical bromelioid fashion, as two bumps at the petal base that flank the antipetalous staminal filament (Fig. 65). The primordia begin to form the thickened ridgelike structure (Fig. 66) before the sac primordia become visible (Figs. 67, 68) at the base of the ridge. The ridge continues to enlarge (Figs. 69–72) as the sac primordia begin to form a cupulate precursor to the sac (Figs. 69–74). Finally, the sac walls begin to elongate and variable amounts of toothing and lobing of the margin develop. The amount of sac-margin ornamentation varies somewhat from flower to flower within the inflorescence. See Figs. 77 and 78 for an example of the extremes of variation found in this study.

Pitcairnia lanuginosa and *Vriesea glutinosa* illustrate petal appendage development in Pitcairnioideae and Tillandsioideae, respectively. Development in these taxa is less complicated than in Bromelioideae. Nearly all known petal appendages in the Pitcairnioideae consist of a single tongue-like appendage per petal. The few known exceptions exist as modified longitudinal folds, or a pair of separate appendages that flank the antipetalous staminal filament (e.g., Smith and Downs, 1974; Varadarajan and Brown, 1988). As mentioned earlier, the primordia for this single appendage originates as two primordial units (Figs. 79, 80) that fuse soon after initiation (Fig. 81). The margin of the developing petal appendage becomes defined (Figs. 82, 83), and the last phase of development involves appendage elongation (Figs. 83, 84), presumably by an intercalary meristem. In the Tillandsioideae the paired petal appendage primordia remain separate (Figs. 85, 86), each producing a single appendage (Figs. 87, 88).

Anther development, relative to the onset of meiosis,

Figs. 15–22. Bromelioideae petal appendages. Bars = 1.0 mm. 15. *Aechmea seideliana*. 16. *Ananas ananassoides* var. *ananassoides*. 17. *Araeococcus flagellifolius*. 18. *Billbergia morelii*. 19. *Aechmea nudicaulis* var. *nudicaulis* (Martinelli 11775). 20. *B. pyramidalis*. 21. *Billbergia* sp. 22. *Fascicularia bicolor*.

Figs. 23–30. Bromelioideae petal appendages. Bars = 1.0 mm. 23. *Hohenbergia correia-arauji*. 24. *Orthophytum fosterianum*. 25. *O. leprosum*. 26. *Pseudoananas sagenarius*. 27. *Quesnelia lateralis*, basal segment of petal. 28. *Q. lateralis*, median segment of petal. 29. *Streptocalyx floribundus*. 30. *Wittrockia* sp.

Figs. 31–38. Pitcairnioideae petal appendages. Bars = 1.0 mm. 31. *Abromeitiella lorentziana*, mature. 32. *A. lorentziana*, early development, postmicrosporogenesis. 33. *Deuterocohnia meziana*. 34. *Pitcairnia lanuginosa*. 35. *P. pulverulenta*. 36. *P. punicea*. 37. *P. xanthocalyx*. 38. *Pitcairnia* sp. (Gilmartin & Betancourt 3107).

Figs. 39–46. Tillandsioideae petal appendages. Bars = 1.0 mm. 39. *Mezobromelia bicolor* (SEL 86-709). 40. *M. fulgens*. 41. *M. lyman-smithii*. 42. *M. bicolor* (Benzing s.n.). 43. *Vriesea apocalyx*. 44. *V. atra*. 45. *V. atro-purpurea*. 46. *V. carinata*.

Figs. 47–54. Tillandsioideae petal appendages. Bars = 1.0 mm. 47. *Vriesea cereicola*. 48. *V. ensiformis*. 49. *V. friburgensis*. 50. *V. geniculata*. 51. *V. gladioliflora*. 52. *V. graminifolia*. 53. *V. incurvata*. 54. *V. malzinei*.

Figs. 55–60. Tillandsioideae petal appendages. Bars = 1.0 mm. 55. *Vriesea maxoniana*. 56. *V. neoglutinosa*. 57. *V. ospinae*. 58. *V. psittacina* var. *rubro-bracteata*. 59. *V. recurvata*. 60. *V. schwackiana*.

was determined for each floral bud in a developmental sequence. The initiation of petal appendages always accompanied or closely followed the onset of meiosis.

Intergeneric hybrids—Three artificial intergeneric hybrids, each with a petal appendaged parent and a non-appendaged parent, were examined. $\times$ *Cryptbergia* ‘Mead’

is a hybrid between *Cryptanthus beuckeri* E. Morren and *Billbergia nutans* Wegland ex Regel (Smith and Read, 1975), and $\times$ *Cryptbergia* ‘Red Burst’ was generated in a cross between *Cryptanthus bahianus* L. B. Smith and *B. nutans* (Smith and Read, 1975). Both parental species are from the Bromelioideae. *Cryptanthus* produces naked petals, while *Billbergia* species bear appendages. More

Figs. 61–64. Tillandsioideae petal appendages. Bars = 1.0 mm. 61. *Vriesea simplex*. 62. *V. viridiflora*. 63. *Vriesea* sp. (SEL 85-1363). 64. *Vriesea* sp. (Martinelli 10921).

specifically, *B. nutans* is described as having “2 large coarsely serrate scales at (the petal) base” (Smith and Downs, 1979). All $\times$ *Cryptbergia* ‘Mead’ and ‘Red Burst’ flowers examined during this study show conspicuous, well-developed petal appendages with coarsely serrate margins (e.g., Fig. 89). Open flowers of $\times$ *Cryptbergia* ‘Mead’ and ‘Red Burst’ appear to be fully functional. However, the ovules abort, and pollen stainability studies using three different stain systems show 0% stainable pollen (Brown, unpublished data).

The $\times$ *Vrieslandsia* cross utilized in the study involved a *Vriesea* hybrid, *V. ‘Marieae’* (= *V. carinata* Wawra $\times$ *V. barilletii* E. Morren) as one parent and *Tillandsia multicaulis* Steudel as the other. A single *Vrieslandsia* individual has been cultivated in the University of Wyoming botany greenhouse for 4 yr. During each of the last 2 yr this plant has produced a single inflorescence. Externally, the inflorescence appears to be normal; however, flowers fail to develop beyond the organ initiation phase. In all cases, the abortive $\times$ *Vrieslandsia* buds contain a full complement of miniature sepals, petals, androecial, and gynoecial parts. Furthermore, the petals from these buds show the presence of two small ridgelike bumps at the

petal base, flanking the antipetalous staminal filament (Fig. 90). The position and appearance of these bumps correspond precisely to the initiation stage for petal appendage primordia observed in numerous species of *Vriesea* (e.g., Fig. 85).

Anatomy—No detailed anatomical evaluation of bromeliad petals and petal appendages was conducted. However, random samples of mature petals and petal appendages from all subfamilies were examined by hand section to study anatomical details. Based on this survey, the bromeliad petal appendage appears to be a nonvascularized, parenchymatous outgrowth of the adaxial petal surface. Studies of bromeliad flowers involving partial serial sections, mostly for the purpose of studying gynoecial structure (Ueno, 1989), also revealed no vasculature in petal appendages.

DISCUSSION

Morphological variability in petal appendages is such that it may be useful, in conjunction with other characters, to delineate species or species alliances. As such, they

Figs. 65–70. *Aechmea filicaulis* petal appendage developmental sequence, part 1. Bars = 1.0 mm, unless otherwise indicated. 65. A-20; petal appendage primordia become visible as two small mounds of tissue flanking the staminal filament (missing). 66. A-19. 67. A-17. 68. A-15; higher magnification of one petal appendage primordium showing base of primordial ridge with initial stages of pouch-primordial development. Bar = 100 μ m. 69. A-14. 70. A-11.

Figs. 71–78. *Aechmea filicaulis* petal appendage developmental sequence, part 2. Bars = 1.0 mm. 71. A-9. 72. A-7. 73. A-7, different petal, closer view of pouch-primordia. 74. A-5. 75. A-4. 76. A-3. 77. A-2. 78. Fully mature anthesis-stage petal appendage.

Figs. 79–84. *Pitcairnia lanuginosa* petal appendage developmental sequence. Bars = 1.0 mm. 79. Petal appendage primordium first visible as two arching ridges. 80. Primordial ridge concrescence. 81–83. Early stages in appendage expansion. 84. Fully mature, anthesis-stage petal appendage.

have been underutilized in bromeliad taxonomy. This is common for most delicate, poorly preserved bromeliad floral features (see Brown and Gilmartin, 1984, for additional discussion of this matter). For instance, the distribution of the fringed-pouch type of petal appendage may be useful in identifying species groups within the notoriously difficult, and probably artificial, genus *Aechmea*. More attention should be devoted to fresh or liquid-

preserved floral features in Bromeliaceae. Some workers (e.g., Utley, 1978, 1983; Gardner, 1983, 1986; Evans and Brown, 1989) have appreciated the value of fresh and/or liquid-preserved bromeliad floral material.

The concern with petal appendages in Bromeliaceae is not over their morphological variability and herein suggested underutilization as a taxonomic character. The concern rests with the great weight that presence vs. ab-

Figs. 85–88. *Vriesea glutinosa* petal appendage developmental sequence. Bars = 1.0 mm, unless otherwise indicated. 85. Petal appendage primordia soon after initiation. 86. Higher magnification of individual petal appendage primordium. Bar = 100 μ m. 87. Early stage in appendage expansion. 88. Mature, anthesis-stage pair of petal appendages.

sence of petal appendages has received in the historical circumscription of certain bromeliad genera (e.g., *Vriesea* and *Tillandsia*).

Petal appendage development in each subfamily has shown that these are the last external, multicellular structures formed in the flower. Their initiation and subsequent maturation coincide with the final maturation and enlargement phase of the flower (Fig. 99). As such, petal appendages in the Bromeliaceae represent terminal ontogenetic characters (Løvtrup, 1978). There are generalizations (e.g., Sachs, 1982) that a structure formed late in ontogeny (i.e., terminal character) is more susceptible to evolutionary change because a modification or reversal in the terminal character will not affect preceding devel-

opmental steps. To use bromeliad petal appendages as an example, these structures could presumably be lost and/or gained repeatedly without affecting the development and function of other floral organs. However, terminal ontogenetic status for a character does not demonstrate homoplasy for that character. It does suggest that homoplasy in that character may be realized more easily, and without impact on the ontogeny of earlier formed, nonterminal characters. Thus, it could be interpreted that these developmental studies support the increasingly popular notion (e.g., Utley, 1978; Benzing, 1980; Brown, 1988; Beaman, 1989) that petal appendages alone are not "good" characters (i.e., synapomorphic) for generic circumscription in Bromeliaceae.

Figs. 89, 90. Petal appendages in intergeneric hybrids involving one parent with petal appendages, and the other parent without petal appendages. Bars = 1.0 mm. 89. $\times$ *Cryptbergia* 'Mead'; fully mature, anthesis stage. 90. $\times$ *Vrieslandsia*; primordia present in abortive flower.

Similarly, it has been observed (Takhtajan, 1954, 1972) and reiterated (Tucker, 1984) that there are strong correlations between the relative value of a character within the Linnean taxonomic hierarchy and the relative timing of the appearance of that character during ontogeny. Characters separating genera tend to be manifested during the "mid-development-determined" (Tucker, 1984; corresponds to the "organogeny" and "form differentiation, enlargement" phases in Tucker, 1988) phase of floral ontogeny. Characters useful in separating species and intra-specific taxa tend to be late or terminal in ontogenetic manifestation (see Tucker, 1984, for full details). The ontogenetic information on bromeliad petal appendages, and the heavy generic level taxonomic emphasis that has been placed on petal appendages in the Bromeliaceae, does not agree with the correlations noted by Takhtajan (1954, 1972) and Tucker (1984). In other words, petal appendages in the Bromeliaceae, by virtue of their ter-

minal ontogenetic nature, would be predicted to have greatest taxonomic utility at the specific or subspecific level.

We examined intergeneric hybrids in hopes of learning something about the genetic basis of petal appendage expression. Information from the $\times$ *Cryptbergia* hybrids is the most useful, because floral morphogenesis is complete. The petal appendages in the $\times$ *Cryptbergia* specimens are very similar to those found in the appendaged parent, *Billbergia*. The *Vrieslandsia* hybrid formed apparent petal appendage primordia at the base of each petal prior to floral abortion. Interpretations from these observations are limited. If petal appendage expression is controlled by a single gene, it would appear that petal appendage presence is dominant. If control is polygenic, the F1 individuals are receiving sufficient genetic information from the parent with petal appendages to exceed the minimum threshold needed for petal appendage expression. Sterility precludes the possibility to explore further the genetic basis of bromeliad petal appendage formation in these hybrids using standard crossing and backcrossing methods. Other intergeneric hybrids involving parents with and without petal appendages need to be studied.

It has been suggested that the petal appendages in the Bromeliaceae are homologous with the corona found in some members of the Velloziaceae (Beaman, 1989; Brown, unpublished data). In a cladistic analysis of bromeliad subfamily relationships, Beaman (1989) selected the Velloziaceae as the probable sister group for outgroup polarization of characters. In his analysis, the petal appendage/corona character serves as one of four synapomorphies used to unite the Bromeliaceae and Velloziaceae as sister taxa. Petal appendages then become symplesiomorphic for the Bromeliaceae.

Within Tillandsioideae, Beaman (1989) considered it likely that petal appendages have been lost independently in *Tillandsia*, *Guzmania*, and *Catopsis* and regained in part of *Vriesea* (subg. *Alcantarea*). One conclusion from Beaman's work is that "Phylogenetic relationships in the Tillandsioideae have been obscured by reliance on certain key characters (e.g., petal appendages) for which parallel evolution or character-state reversals surely have been a factor."

Gilmartin and Brown (1987), in a soundly criticized cladistic analysis of Bromeliaceae relationships (see Simpson, 1988; Gilmartin and Brown, 1988), concluded that Velloziaceae are the probable sister taxon to Bromeliaceae. *rbcL* sequence data generated by Clark and Clegg (1990) and incorporated into an expanded cladistic analysis by Duvall et al. (1991) confirm the monophyletic status of Bromeliaceae, but show Rapatiaceae, and not Velloziaceae, to be the sister taxon to Bromeliaceae. Detailed reevaluation of Velloziaceae corona characteristics

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Figs. 91–98. Bars = 1.0 mm, unless otherwise indicated. 91. Septal nectary pore at base ovary; *Vriesea gladioliflora* (DB s.n.). Bar = 100 μ m. 92. Higher magnification of septal nectary pore in Fig. 91. Bar = 10 μ m. 93. Cross section of near anthesis floral bud, at level just above the distal tips of the petal appendages; *Vriesea recurvata*. 94. *Vriesea maxoniana*; longitudinal section through petal and one petal appendage; note staminal filament and possible nectar-pooling chamber between the base of the petal and gynoecium. 95. *Aechmea contracta*; cross section of mature flower at level just above the roof of the ovary. Note three nectar pores, also hollow style. 96. *Aechmea serrata* cross section of near anthesis flower, at level just above the distal tips of the petal appendages. 97. *Aechmea nudicaulis* (Martinelli 11775), near medial longitudinal section of anthesis stage flower. 98. *Quesnelia lateralis*, medial longitudinal section of near anthesis-stage flower.

Fig. 99. Floral bud growth in *Aechmea filicaulis*. Bud age corresponds to bud/flower position in the inflorescence. Numbers associated with point locations (i.e., 65–78) refer to Fig. numbers illustrating petal appendage development.

(e.g., de Menezes and Semir, 1990), in light of what is now known about bromeliad petal appendages, tends to support these molecular data, and the lack of homology between Bromelioideae petal appendages and the corona of Velloziaceae.

Very little data exist concerning bromeliad pollination biology and the role that specialized floral structure might play in the overall function of the bromeliad flower. It has been suggested that ornithophily may be modal for the family (Utley, 1978; Benzing, 1980; Gardner, 1983). Harms (1930) proposed that bromeliad petal appendages help prevent nectar loss. McWilliams (1974) proposed that the appendages are involved in determining the height at which nectar is held in the flower. Benzing's (1980) review led him to conclude that petal scales are of equivocal significance. Varadarajan (1986; Varadarajan and Brown, 1988) concluded that petal appendages are vestigial and appear to be nonfunctional in some pitcairnioid taxa, and function as "nectariferous scales" that aid in nectar retention in other pitcairnioids.

We suggest that bromeliad petal appendages are most probably involved in intrafloral nectar management (e.g., nectar retention, presentation, delivery). Extensive studies of Bromelioideae gynoecia (Ueno, 1989) and sepal nectaries (Bohme, 1988) have demonstrated the locations for the duct and pore systems needed to deliver sepal nectary products to the intrafloral spaces. In taxa with a superior gynoecium (i.e., Pitcairnioideae, Tillandsioideae) the nectar-release pores are located in the base of the gynoecial sutures (Figs. 91, 92), with one pore per suture. Taxa in the Bromelioideae have an inferior ovary, and there are three nectar-release pores located on the floor of the hypanthium (Fig. 95). In all subfamilies the nectar-release pores are opposite the antipetalous stamen. Utley (1983), Brown (personal observation), and Luther (Selby Botanical Gardens, Sarasota, FL, personal communication) note that petal appendages loosely partition the intrafloral chamber into two compartments (Figs. 93, 94, 96–98) that can be designated capillary-space and noncapillary-space. In hypogenous flowers with petal appendages, the capillary-space is located between the outer

surface of the ovary wall and the adaxial surfaces of the petal appendages and adjacent staminal filaments (Fig. 93). In Bromelioideae flowers the capillary-space is delineated by the inner hypanthium floor, wall, and the petal appendages (Figs. 96–98). Fahn (1952) has stressed the importance of capillary-space between the ovary and staminal/petal bases in the retention of nectar, especially for horizontal to inclined flowers. The retention of a substantial volume of nectar per flower is consistent for taxa where most of the presumed pollinators (e.g., birds, bats) have high energy requirements.

Other functions for bromeliad petal appendages are possible, including feeding-part (e.g., tongue) guides and protection against nectar desiccation. If petal appendages do in fact have a function, or functions, in the pollination biology of bromeliads, demonstration of this will require a substantial effort.

The continued recognition of generic-level distinctions predicated on the presence or absence of petal appendages is probably unwarranted for Bromeliaceae, and especially for Tillandsioideae. Concerted efforts are needed to re-evaluate characters and character correlations, identify new or underutilized characters, and generate new data sets in an effort to produce better (i.e., phylogenetic) classifications in the Bromeliaceae. While the results of this study challenge the current practice of circumscribing certain bromeliad genera based on petal appendage occurrence, they provide no better alternatives. The monograph by Smith and Downs (1974, 1977, 1979) is an important synthesis, and merits maintenance until data become available that can support realignments and new circumscriptions in a phylogenetic context. We neither propose nor condone any purely nomenclatural changes as a result of this work.

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