MORPHOLOGICAL VARIATION OF SOME FLORAL FEATURES OF THE SUBFAMILY PITCAIRNIOIDEAE (BROMELIACEAE) AND THEIR SIGNIFICANCE IN POLLINATION BIOLOGY

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Scanning electron and light microscopy observations of wet-preserved flowers of Bromeliaceae subfamily Pitcairnioideae yield new information on the stigma, petal scales, and sepal nectaries. Variations of the stigma types are evident among several genera. The gross structural features of the stigma do not indicate definite pollination trends, but the shape of the lobes and papillae indicate a few specific modes. In pitcairnioid genera, petal scales, when functional, may aid in pollination by accumulating the nectar secreted from the ovary, thus facilitating its availability to the pollinator. Nectaries associated with the gynoecia usually display tripartite channels in the ovary septa. Some developmental changes of the channel structure and position of the ovary indicate three probable modes of nectar release from the gynoecia of the pitcairnioids: (1) through lateral grooves or openings, (2) partly through the apical orifices and partly through the dissolved areas of the spetal channels, and (3) exclusively through the apical orifices. Analysis of a wide range of floral features indicates that ornithophily, chiropterophily, and entomophyly exist in different Pitcairnioideae lineages.

Introduction

Investigations on Bromeliaceae have produced descriptive and systematically useful data (Brown and Gilmartin 1984; Brown et al. 1984; Varadarajan and Brown 1985; Gilmartin and Brown 1985, 1986; Varadarajan 1986a; Varadarajan and Gilmartin 1988), and because of its primitive status, the subfamily Pitcairnioideae was a major focus (Smith 1934; Marchant 1967; Tomlinson 1969; Benzing 1980; Gilmartin and Brown 1987). Mostly, the gynoecial traits of Bromeliaceae were described, with a little information on the floral features of the Pitcairnioideae (Gardner 1982; Utley 1983; Brown and Gilmartin 1984; Gilmartin and Brown 1985).

Several floral characteristics (petal scales, nectaries) were described only from dried and rehydrated material, which was partly responsible for the poor structural detail of floral traits. Petal scales (ligule, petal appendages, nectariferous scales, lateral folds, vertical calli) are relatively frequent in Bromeliaceae and are diagnostic of several genera (Mez 1934–35; Smith and Downs 1974, 1977, 1979). Aside from the taxonomic value associated with petal scales, their morphological variation and significance in pollination were not well elucidated.

Gynoecia of the monocotyledons often contain nectaries in the ovary septa (sepal nectaries) and are known to be of taxonomic value in several families (Daumann 1970; Fahn 1982; Thorne 1983; Dahlgren et al. 1985). Budowski’s (1922) examination represents the only major study of Bromeliaceae septal nectaries. Their morphological variation and the significance in pollination were not analyzed until the present work.

The goal of this study is to examine the diversity of stigma morphology, petal scales, and sepal nectaries of the subfamily Pitcairnioideae from wet-preserved material.

Material and methods

The 41 species of nine genera of Pitcairnioideae were examined by light microscopy; 30 species were also examined with scanning electron microscopy (SEM) (table 1). All material was field-collected by G. S. Varadarajan and preserved in FAA (formaldehyde:acetic acid:ethanol, 1:1:18). Samples of stigmas and ovaries were selected from pre-anthesis to post-anthesis, and the internal structure of ovaries was examined from freehand cross sections. Petal scales were examined from nearly mature (anthesis) flowers.

Floral parts selected for SEM were transferred from FAA to 0.1 M cacodylate buffer, postfixed in OsO4, dehydrated through an ethanolic series (30%, 50%, 70%, 95%, 100%), dried in a Bomar critical-point dryer, mounted on aluminum stubs, and gold coated with a Technics Hummer-Sputter coater. Flower samples were then examined in an ETEC Auto Scan U-1 scanning electron microscope at 20 kV.
Results and discussion

FLORAL FEATURES OF PITCAIRNIOIDEAE

STIGMA MORPHOLOGY.—Terminology of the stigma types follows Brown and Gilmartin (1984). The most commonly observed stigma type in the subfamily is the conduplicate-spiral pattern, type II (figs. 1–6, 8–11). The simple-erect type I occurs in Brocchinia, Cottendorfa, and Fosterella. The convolute-blade stigma, type III, previously reported only from the subfamily Tillandsioideae, occurs in Navia (fig. 7).

Stigma types vary within themselves as well as within certain taxa; e.g., species of Brocchinia exhibit types I and II (table 2). We confirm reports of a modified conduplicate-spiral type (type II) in

Fig. 1, Ayensua uapanensis (Varadarajan 1196). Type II stigma. Arrow indicates asymmetric lobe of stigma. Note bulbous papillae (BP) and spiraling restricted to individual lobes. Figs. 2, 3, Brocchinia acuminata (Varadarajan & Oliva 1159). Two views of a type II stigma. Note tubular, branched papillae (TP). Fig. 4, Dyckia brevifolia (SEL 82-558). Type II stigma at pre-anthesis. Arrows indicate highly compact stigma lobes. Fig. 5, Deuterocohnia schreiteri (Varadarajan et al. 1247). Type II stigma during post-anthesis. Note pollen grains trapped within dissected lobes (DL) of stigma branches. Compare with papillae in other taxa.
Figs. 6–9.—SEM of variation in stigma morphology. Fig. 6, Dyckia ragonesei (Varadarajan 1218). Type II stigma at post-anthesis, displaying the loosened stigmatic lobes. Note dissected areas (DL) of stigma lobes with pollen (P). Fig. 7, Navia splendens (Varadarajan 1215). Type III stigma during anthesis with convolute blades (CB); Fig. 8, Pitcairnia nuda (SEL 81-1979). Type II stigma during anthesis. Spiral folding involves mostly the individual lobes. Tubular papillate outgrowths (TP). Fig. 9, Pitcairnia heterophylla (Varadarajan 1171). Type II stigma during anthesis with noticeable spiral folding of individual lobes and entire stigmatic apparatus. Bulbous papillae (BP) are confined to edges of stigma lobes.
B. acuminata (figs. 2, 3) and of a weakly conuplicate-spiral type in B. gilmartinii (VARADARAJAN 1986b). The stigma of B. steyermarkii is similar to type I reported in B. reducta Baker (BROWN and GILMARTIN 1984).

Variability in types I and II is evident with regard to the (1) papillae on the lobes, (2) presence of twisted or spiraled branches, (3) duration of the spiral folding, and (4) shape and symmetry of the individual lobes.

PAPILLAE.—Stigma lobes of some taxa are associated with relatively small, simple, bulbous structures known as the papillae (fig. 11). These are occasionally tubular (fig. 8), complex, and
### Table 1

| Taxa                                             | Details of voucher | Locality                                      |
|--------------------------------------------------|--------------------|-----------------------------------------------|
| **Ayensua:**                                     |                    |                                               |
| *A. uaipanensis* L. B. Smith\*                   | Varadarajan 1196   | Venezuela: Bolivar, Auyan Tepui               |
| **Brochonia:**                                   |                    |                                               |
| *B. acuminata* L. B. Smith*                      | Varadarajan & Oliva 1159 | Venezuela: Bolivar, La Escalera             |
| *B. gilmartini* Varadarajan et al.                | Varadarajan & Oliva 1158 | Venezuela: Bolivar, La Escalera             |
| *B. steyermarkii* L. B. Smith*                   | Varadarajan & Oliva 1164 | Venezuela: Bolivar, La Gran Sabana          |
| **Cottendorfia:**                                |                    |                                               |
| *C. guianensis* Kl. ex Bak.
   \*                                      | Varadarajan & Oliva 1161 | Venezuela: Bolivar, Kavanayan               |
| **Deuterocohnia:**                               |                    |                                               |
| *D. haumantii* Castell.\*                        |                    | Argentina: Salta, Cafayate                   |
| *D. longipetala* Mez.\*                         | Varadarajan et al. 1250 | Argentina: Cordoba, Sierra Chica          |
| *D. schreiteri* Castell.\*                      | Varadarajan et al. 1248 | Argentina: Salta, Cafayate                   |
| **Dyckia:**                                      |                    |                                               |
| *D. brevifolia* Bak.
   \*                                      | SEL 82-558\*        | Brazil                                        |
| *D. niederleiini* Mez.\*                        | GSV 0030\*         | Brazil                                        |
| *D. ragonesei* Castell.\*                       | Varadarajan 1218   | Argentina: Entre Rios Rio Parana            |
| **Fosterella:**                                  |                    |                                               |
| *F. elata* Luther\*                             | Holotype\*         | Bolivia                                        |
| *E. penduliflora* L. B. Smith\*                 | SEL 024397\*       | Peru                                          |
| **Navya:**                                       |                    |                                               |
| *N. splendens* L. B. Smith\*                    | Varadarajan 1215   | Venezuela: Bolivar, Auyan Tepui               |
| **Pitcairnia:**                                  |                    |                                               |
| *P. andreana* Linden\*                          | SEL 82-554\*       | Colombia                                      |
| *P. armata* Maury\*                             | Varadarajan & Gaunchez 1150 | Venezuela: T. F. Amazonas, P. Auyacucho   |
| *P. brevicalycina* Mez.\*                       | Varadarajan & Ortega 1156 | Venezuela: Trujillo, Bocono                 |
| *P. bulbosa* L. B. Smith\*                      | Varadarajan & Guanchez 1143 | Venezuela: T. F. Amazonas, P. Auyacucho   |
| **P. corallina** Linden & Andre                  | Varadarajan 1192   | Colombia                                      |
| *P. crassa* L. B. Smith                         | Varadarajan et al. 1292 | Bolivia: Nor-Yungas                         |
| *P. ctenophylla* L. B. Smith\*                  | Varadarajan 1195   | Venezuela: Bolivar, Auyan Tepui               |
| *P. heterophylla* Bae\*                         | Varadarajan & Oliva 1171 | Venezuela: Aragua, Pittier Natl. Park      |
| *P. meridensis* Kl. ex Mez.\*                   | Varadarajan et al. 1176 | Venezuela: Merida, Parque de Colorados     |
| *P. nubigena* Planch. & Linden                   | Varadarajan et al. 1181 | Venezuela: Merida, La Carbonero        |
| *P. nuda* Baker\*                               | SEL 81-1979\*       | Surinam                                       |
| *P. paniculata* R. & P.                         | Varadarajan et al. 1281 | Bolivia: Nor-Yungas, Yalosa                |
| *P. pruinosa* H. B. K.\*                        | Varadarajan & Guanchez 1147 | Venezuela: T. F. Amazonas, P. Auyacucho   |
| *P. pungens* H. B. K.                           | SEL 016687\*        | Ecuador                                       |
| *P. pinacea* Scheid.                            | SEL 80-1590\*       | Mexico                                        |
| **Puya:**                                        |                    |                                               |
| *P. aristeguietia* L. B. Smith\*               | Varadarajan et al. 1188 | Venezuela: Tachira,Paramo de Zambador     |
| *P. atra* L. B. Smith                           | Varadarajan et al. 1274 | Bolivia: Sud-Yungas, Unduavi                |
| *P. ferruginea* L. B. Smith\*                   | Varadarajan et al. 1272 | Bolivia: La Paz, La Florida                |
| *P. floccosa* E. Morr. ex Mez.\*                | Varadarajan & Oliva 1163 | Venezuela: Bolivar, La Gran Sabana         |
| *P. harmsii* Castell.\*                         | Varadarajan et al. 1245 | Argentina: Tucuman, Tafi del Valle       |
| *P. laza* L. B. Smith\*                         | SEL 83-207\*        | Bolivia                                       |
| *P. liloi* Castell                            | Varadarajan 1229   | Argentina: Salta, El Tala                   |
| *P. mirabilis* L. B. Smith\*                    | Varadarajan 1230   | Argentina: Salta Rio Blanco                 |
| *P. pearcei* Mez.\*                            | Varadarajan et al. 1286 | Bolivia: Nor-Yungas, Yalosa                |
| *P. stenothyriso* Mez.                          | Varadarajan & Canne 1310 | Bolivia: La Paz, Sorata                  |
| *P. trianae* Bak.                               | Varadarajan et al. 1189 | Venezuela: Tachira, Paramo de Zambador     |
| *P. tristis* L. B. Smith\*                      | Varadarajan & Canne 1306 | Bolivia: Cochabamba, Tiraque              |

**Note.**—Voucher specimens in LAB, LAP, MO, PORT, SEL, US, VEN, and WS.

* Taxa processed for SEM

* Taxa cultivated at the Selby Botanical Gardens, Florida.
TABLE 2  
TAXONOMIC DISTRIBUTION OF THE STIGMA TYPES  
in the Subfamily Pitcairnioideae

| Genera       | No. species examined | Stigma type(s)* |
|--------------|----------------------|-----------------|
| Ayensua      | 1                    | II              |
| Breccaria    |                      | (I')            |
| Brocchinia   | 3                    | I (I', II)      |
| Cottendorfia | 1                    | II              |
| Deuterocohnia| 3                    | 2 (I', II')     |
| Dyckia       | 3                    | II (I, II')     |
| Fosterella   | 2                    | I (I')          |
| Hechtia      |                      | (I, II')        |
| Navia        | 1                    | III (flabelliform [III?']) |
| Pitcairnia   | 15                   | II (II')        |
| Puya         | 12                   | II (II')        |
| Steyerbromelia|                    | (II')           |

**NOTE.**—Stigma types are unknown for Abromeitiella and Connellia. Stigma types indicated in parentheses include other reports.

* Definition according to Brown and Gilmartin (1984).
* From Smith (1984).
* From Mez (1934–1935).
* From Brown and Gilmartin (1984).

branched (figs. 2, 3). Papillae are distinguished from the dissected or lacerated portions of the stigma (fig. 5) and are not discernible until anthesis (fig. 10). At post-anthesis, the papillae are characterized by a moist, sticky surface entangled with pollen.

**COMPACTION OF THE STIGMA BRANCHES.**—Describing the degree of compaction of stigma lobes is very subjective as it depends on the size and shape of the individual lobes. Two general types of compaction of the lobes are characterized during anthesis. In the first type, the individual lobes are conduplicately folded (figs. 1, 8) with little or no spiraling of the whole stigmatic apparatus. In the second type, conduplication of the lobes is highly compact and involves the lobes as well as the entire stigma unit in the spiral folding (fig. 11).

**DURATION OF THE SPIRAL FOLDING.**—Compaction and spiral folding of the lobes begin prior to anthesis (figs. 1, 9, 11), are completed during stigma receptivity, and are relaxed at post-anthesis (figs. 5, 6). Because of these structural changes during development, one must exercise caution in interpreting stigma morphology.

**SHAPE AND SYMMETRY OF THE INDIVIDUAL LOBES.**—Stigma branches may be ovate (fig. 3), lanceolate, spathulate (fig. 9), or sagittate (fig. 6), and in some stigmas, one of the lobes is asymmetric because of a slight extension of one limb (fig. 1).

**PETAL SCALES.**—Petal scales are diagnostic for Abromeitiella, Breccaria, and Deuterocohnia. Yet, they show a high degree of instability in occurrence, especially among the species and populations of several Pitcairnia and Puya species (Pitcairnia pulverulenta R. & P., P. schultzei Harms, Puya hofstienii Mez). Petal scales generally occur at the bases of petals (figs. 12–22) and may have originated from simple vertical folds along the interior face of the petal (e.g., Puya floccosa; fig. 14). Petal scales may be a pair of earlike lobes (fig. 15) flanking the base of the filaments near petal margins. More often, petal scales are solitary, oblong, and tongue-shaped with variable sizes, as in several species of Pitcairnia (fig. 16). Occasionally, petal scales develop crenations (figs. 17, 18) or lacerations (figs. 12, 13) or complex distal modifications (figs. 20–22).

Figs. 14–22.—Diagrams illustrating the variable morphology of petal scales. Figs. 17 and 20–22 are reproduced from Smith and Downs (1974), with permission copyright 1974, the New York Botanical Garden. Fig. 14, Puya floccosa (Varadarajan & Oliva 1163). Petal scales represented as vertical folds (arrows) on the interior of petals. Figs. 15–22, diversity of petal scales in Pitcairnia. Fig. 15, P. brevicalycina (Varadarajan & Ortega 1156); fig. 16, P. crassa (Varadarajan et al. 1292); fig. 17, P. caricifolia; fig. 18, P. meridensis (Varadarajan et al. 1176); fig. 19, P. nubigena (Varadarajan et al. 1181); fig. 20, P. heterophylla; fig. 21, P. pungens; fig. 22, P. filispina.
SEPTAL NECTARIES.—The sepal nectaries of Bromeliaceae correspond to the “labynthine common nectarial cavity” type sensu SCHMID (1985). Architecture of the sepal nectaries varies in superior and inferior ovaries (BUDNOWSKI 1922). Pitcairniaoid flowers are uniquely suited for examining this variation as the ovaries range from fully superior to completely inferior. Septal nectaries of pitcairniosids usually consist of three longitudinal systems of channels in the septa that are connected with the axis by a median component (figs. 24, 26). The channels originate at the ovary base and open through orifices at the top. The orifices are small slits or rounded pores (BUDNOWSKI 1922). Triradiate channels sometimes extend to the style and exhibit vertical folds and twists, appearing as convolutions, branches, and undulations in some cross sections (fig. 25). The surface of the sepal nectaries is lined by variable amounts of glandular tissue. Glandular tissue and the contents of the secretion of Pitcairnioidae may correspond to those of some Liliaceae members (FAHN 1949, 1952; FAHN and BENOUAICHE 1979).

Our observations of the sepal nectaries from representatives of Pitcairnioidae with superior, semi-inferior, and inferior ovaries confirm some structural variations reported by BUDNOWSKI (1922), e.g., the number of nectariferous channels, orifices. In taxa with superior ovaries (Deuterocohnia schreiteri, Dyckia ragonezei, and Fosterella elata), six nectariferous channels are discernible radially during the very early stages of flower development. Three channels oriented toward the sepal probably constitute the primary nectariferous system. The remainder, oriented toward the placenta, may be the secondary nectariferous system (fig. 24). The latter channels are discernible only in the ovaries of pre-anthesis flowers. In some superior ovaries (Navia splendens, Cotterodifia guianensis) and semi-inferior to inferior ovaries (Pitcairnia heterophylla, Puya harmsii, fig. 27), the nectaries include only the sepal channels in all developmental stages examined.

The number, orientation, persistence of the nectariferous channels, and ovary position indicate three modes of nectar release from the ovary. In superior ovaries with six radial channels or three sepal channels (fig. 27), nectar release to the exterior by the dissolution of the sepal channels seems likely. The ovary surface is mostly grooved, and the sepal channels break open at the grooves (figs. 23, 28). Guided by the grooves, nectar flows from the sepal channels to the ovary base, where it finally accumulates.

Placental channels lose their morphological identity at anthesis as they become integrated with the placental tissue. Although the actual route of nectar flow from these channels is not well understood, it appears that their secretions are partly (1) transferred into the locule via the placental tissue and (2) through the dissolved areas of the sepal channels (fig. 28). From the locule, nectar flows through the apical orifices of the ovary. The dissolution of the sepal channels causes the individual carpels to part from one another, leading to a superficial apocarpy (fig. 28).

Nectar release from the semi-inferior/inferior
ovaries is slightly different from the above account. Complete epigny results from the receptacular tissue overgrowing the ovary, beyond the level of origin of the gynoecium (ESAU 1977). Sometimes, the relative position of the inferior ovary is further complicated by the development of an epigynous tube (e.g., Ayensua). All the pitcairnioid inferior ovaries investigated have only three septal channels. Unlike the superior ovaries, the receptacular tissue peripheral to the ovary wall and sometimes the epigynous tube of an inferior ovary are conceivably the main barrier to the nectar flow to the exterior. The only remaining outlet for the nectar of these semi-inferior or inferior ovaries is, therefore, the apical orifices. Persistence of the septal channels during the post-anthesis stages of the inferior ovaries provides evidence for the above explanation.

**FLORAL MORPHOLOGY AND OBSERVATIONS ON THE POLINATION BIOLOGY**

Type II stigma of Pitcairnioideae varies so widely that more than a single pollination system seems probable. The highly compact, condupliquately folded, spatulate stigma lobes (fig. 11) with dense papillae are frequent in relatively large (often 6 cm long), tubular, scarlet to red, zygomorphic flowers of Pitcairnia with abundant nectar (P. corallina, P. meridensis, P. nubigena). These features, in combination with a fairly compact type II stigma, diurnal anthesis, tubular and/or reflexed flowers, hard flower wall, stiff filaments, and stylar base strongly indicate bird pollination (PROCTOR and YEO 1972).

Type II stigma with semicompact lobes with or without papillae (fig. 1) also occurs in large, night blooming, white, tubular blossoms. These actinomorphic flowers occasionally produce strong odors at night and are aggregated on massive, terminal inflorescences conspicuously demarcated from the surrounding foliage (Ayensua uaipanensis, Puya aristeguietae). These features indicate bat pollination (PROCTOR and YEO 1972).

Type I or type II stigmas with ovate to lanceolate, somewhat loosely folded stigma lobes lacking papillae (fig. 5) are characteristic of several relatively small (often 5 cm long), diurnal, white, yellow, green, actinomorphic flowers with moderate amounts of nectar. These flowers are mostly produced on lax, panicked inflorescences (B. steyermarkii, C. guianensis, Deuterocohnia longipetala, D. schreiteri, F. elata, Pitcairnia brevicalycina) and may indicate insect pollination (PROCTOR and YEO 1972).

The degree of compaction of the lobes and papillae may be more reliable in indicating a specific pollination type than the gross morphological type of stigma, especially when considered in conjunc-
tion with the inflorescence, blooming times, flower color, and symmetry.

Petal scales and sepal nectaries provide some indirect clues as to the nectar production, storage, and release associated with some pollination types. McWilliams (1974) suggested that petal scales may help in keeping the nectar in suitable position within the floral tube for the pollinator. However, our observations suggest that, while some petal scales are apparently "nectariferous," others are vestigial.

*Pitcairnia brevicalycina* has yellow flowers with or without petal scales (fig. 15). Three populations of this species examined in Venezuela displayed a simple type of petal scales (fig. 14), accumulating little nectar. In contrast, *P. heterophylla*, a taxon widely known from several areas of tropical America, has scarlet-red flowers with petal scales (fig. 20) and abundant nectar. Although the amount of nectar was determined by crude methods, it is apparent that modes of pollination differed in the two species. The former, with a relatively simple type of petal scales and low amounts of nectar, may be a bee flower; the latter, with a petal scale with complex distal modifications and abundant nectar, may be a moth flower. While petal scales could possibly assist in accumulating nectar in *P. heterophylla*, they may be simply vestigial in *P. brevicalycina* (VARADARAJAN 1987).

Complexity of petal scale morphology does not necessarily provide reliable indications for nectar storage capacity. Even a pair of simple vertical folds on petals of some *P. floccosa* populations (fig. 14) may be nectariferous, although they apparently lack any glandular linings. Other floral structures may substitute for petal scales for storing the nectar. This is indicated by the coherent, swollen filament bases of *Dyckia* that possibly function as a nectar storage site in the absence of petal scales.

Septal and placental nectaries of Bromeliaceae, examined by Budnowski (1922) primarily from a taxonomic viewpoint, were not elucidated from the perspective of pollination. Septal nectaries constitute the internal secretory and storage system of nectar especially significant to the bromeliad blossoms adapted to entomophily, ornithophily, and chiropterophily (MEEUSE 1961; FAEGRI and VAN DER PUL 1971; PROCTOR and YEO 1972). The possible differences in modes of nectar release from well-developed nectariferous system(s), evident in varying ovary positions, associated with a wide range of zygomorphic, tubular, colored flowers (*Pitcairnia* and *Puya*) are apparently linked to bird or bat pollination (VARADARAJAN 1986a, 1987).

McWilliams (1974) listed the studies dealing with hummingbird pollination of bromeliads. Read (1969) documented hummingbird pollination in one *Pitcairnia* species and Snow and Snow (1980) in another. Rees and Roe (1980) discussed the nutritional relationships between birds and *Puya*. In addition, there are several instances in Pitcairnioideae where the strategies for entomophily and chiropterophily are evident. In *Abromeitiella*, *Brockchia*, *Cottendorfia*, *Deuterochoncha*, *Dyckia*, *Fosterella*, and a few other genera, insect pollination may be widespread. Within *Pitcairnia* and *Puya*, however, a wide range of floral features (massive, cylindrical inflorescences, reflexed flowers, zygomorphy, epigyny, carination of sepals) strongly indicates a variety of pollination mechanisms. These are perhaps significant in the adaptive radiation of *Pitcairnia* and *Puya* extensively in South America.

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LITERATURE CITED

BENZING, D. H. 1980. The biology of the bromeliads. Mad River Press, Eureka, Calif.

BROWN, G. K., and A. J. Gilmartin. 1984. Stigma structure and variation in Bromeliaceae-neglected taxonomic characters. Brittonia 36:364–374.

BROWN, G. K., G. S. Varadarajan, A. J. Gilmartin, and H. Luther. 1984. Chromosome reports, Bromeliaceae. Taxon 33:759–759.

Budnowski, A. 1922. Die Septaldrüsen der Bromeliaceen. Bot. Arch. 1:47–80.

Dahlgren, R., T. H. Clifford, and P. F. Yeo. 1985. The families of the monocotyledons: structure, evolution and taxonomy. Springer, Berlin.

Dau mann, E. 1970. Das Blütennektarium der Monocotyledo nen unter besonderer Berücksichtigung seiner systematischen und phylogenetischen Bedeutung. Feddes Repert. 80:463–590.

ESAU, K. 1977. Anatomy of seed plants. 2d ed. Wiley, New York.

FAEGRI, K., and L. Van der PUL, 1971. The principles of pol lination ecology. Pergamon, New York.

FAPIN, A. 1949. Studies in the ecology of nectar secretion. Pales.
J. Bot. Jerusalem 4:207–224.
———. 1952. On the structure of floral nectaries. Bot. Gaz. 113:464–470.
———. 1982. Plant anatomy. Pergamon, New York.
Fahn, A., and P. Benouaiche. 1979. Ultrastructure, development and secretion in the nectary of banana flowers. Ann. Bot. 44:85–93.
Gardner, S. 1982. A systematic study of Tillandsia subgenus Tillandsia. Ph.D. diss. Texas A&M University, College Station.
Gilmartin, A. J., and G. K. Brown. 1985. Cleistogamy in Tillandsia capillaris (Bromeliaceae). Biotropica 17:256–259.
———. 1986. Cladistic tests of hypotheses concerning evolution of xerophytes and and mesophytes within Tillandsia subg. Phytarrhiza (Bromeliaceae). Am. J. Bot. 73:387–397.
———. 1987. Bromeliaceae, related monocots and resolution of relations among Bromeliaceae subfamilies. Syst. Bot. vol. 12 (in press).
McWilliams, E. 1974. Evolutionary ecology. Pages 40–55 in L. B. Smith and R. J. Downs, eds. Pitcairnioideae. Flora Neotropica. Monogr. 14. Hafner, New York.
Marchant, C. J. 1967. Chromosome evolution in Bromeliaceae. Kew Bull. 21:161–168.
Meuse, B. J. D. 1961. The story of pollination. Ronald, New York.
Miz, C. 1934–1935. Bromeliaceae. Pages 1–167 in A. Engler, ed. Das Pflanzenreich. Vol. 4, pt. 32. Engelmann-Cramer, Weinheim.
Proctor, M., and P. Yeo. 1972. The pollination of flowers. Taplinger, New York.
Read, R. W. 1969. Variation and taxonomy of Pitcairnia (Bromeliaceae) in Jamaica. Brittonia 21:83–90.
Rees, W. E., and N. A. Roeg. 1980. Puya raimondii (Pitcairnioideae, Bromeliaceae) and birds: an hypothesis on nutrient relationships. Can. J. Bot. 58:1262–1268.
Schmid, R. 1985. Functional interpretations of the morphology and anatomy of sepal nectaries. Acta Bot. Neerl. 34:125–128.
Smith, L. B. 1934. Geographical evidence on the lines of evolution in Bromeliaceae. Bot. Jahrb. 66:446–468.
———. 1984. Bromeliaceae. Pages 8–48 in J. Steyermark et al., eds. Nuevos Taxa de la Guayana Venezolana. Acta Bot. Venezuela. Vol. 4. Caracas.
Smith, L. B., and R. J. Downs. 1974. Bromeliaceae (Pitcairnioideae). Flora Neotropica. Monogr. 14 (i). Hafner, New York.
———. 1977. Bromeliaceae (Tillandsioideae). Flora Neotropica. Monogr. 14 (ii). Hafner, New York.
———. 1979. Bromeliaceae (Bromelioideae). Flora Neotropica. Monogr. 14 (iii). Hafner, New York.
Snow, D. W., and B. K. Snow. 1980. Relationships between hummingbirds and flowers in the Andes of Colombia. Bull. Br. Mus. Nat. Hist. (Zool.). 38:105–139.
Thorne, R. F. 1983. Proposed new realignments in the angiosperms. Nordic J. Bot. 3:85–117.
Tomlinson, P. B. 1969. Commelinales-Zingiberales. Pages 192–294 in C. R. Metcalfe, ed. Anatomy of the monocotyledons. Vol. 3. Oxford University Press, London.
Utley, J. 1983. A revision of the Middle American theco-phylloid vrieseas (Bromeliaceae). Tulane Stud. Zool. Bot. 24:1–81.
Varadarajan, G. S. 1986a. Taxonomy and evolution of the subfamily Pitcairnioideae (Bromeliaceae). Ph.D. diss. Washington State University, Pullman.
———. 1986b. A new species of Brocchinia Schultes (Bromeliaceae) from Venezuela. J. Brom. Soc. 36:251–254.
———. 1987. Explorations for Pitcairnioideae in South America. I. J. Brom. Soc. 37:16–25.
Varadarajan, G. S., and G. K. Brown. 1985. Chromosome numbers of Pitcairnioideae (Bromeliaceae). Taxon 34:729.
Varadarajan, G. S., and A. J. Gilmartin. 1988. Foliar scales of the subfamily Pitcairnioideae (Bromeliaceae). Syst. Bot. vol. 13 (in press).