

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 septal 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 entomophily 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 (septal nectaries) and are known to be of taxonomic value in several families (DAUMANN 1970; FAHN 1982; THORNE 1983; DAHLGREN et al. 1985). BUDNOWSKI'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 septal 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.

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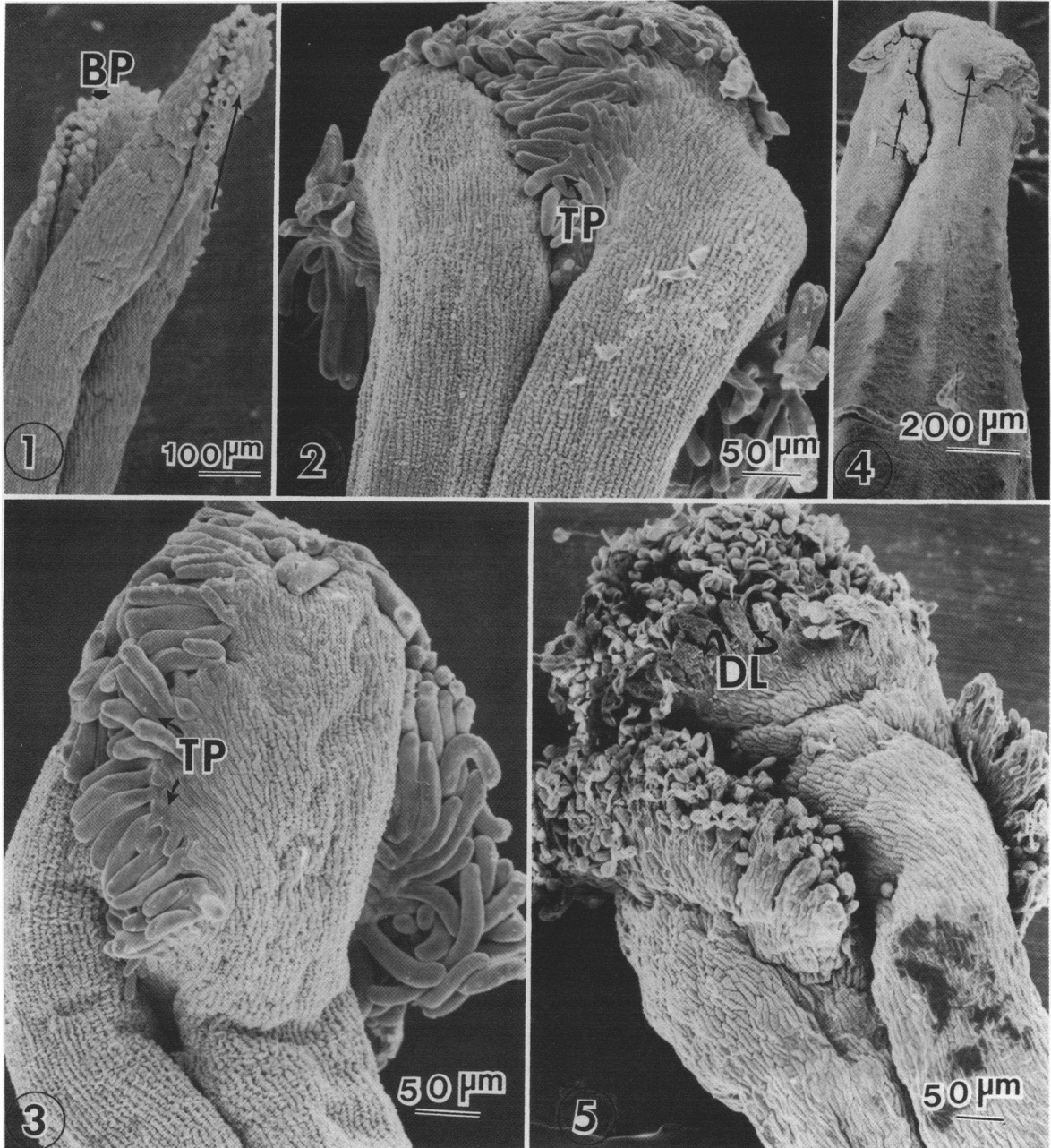
Results and discussion

FLORAL FEATURES OF PITCAIRNIOIDEAE

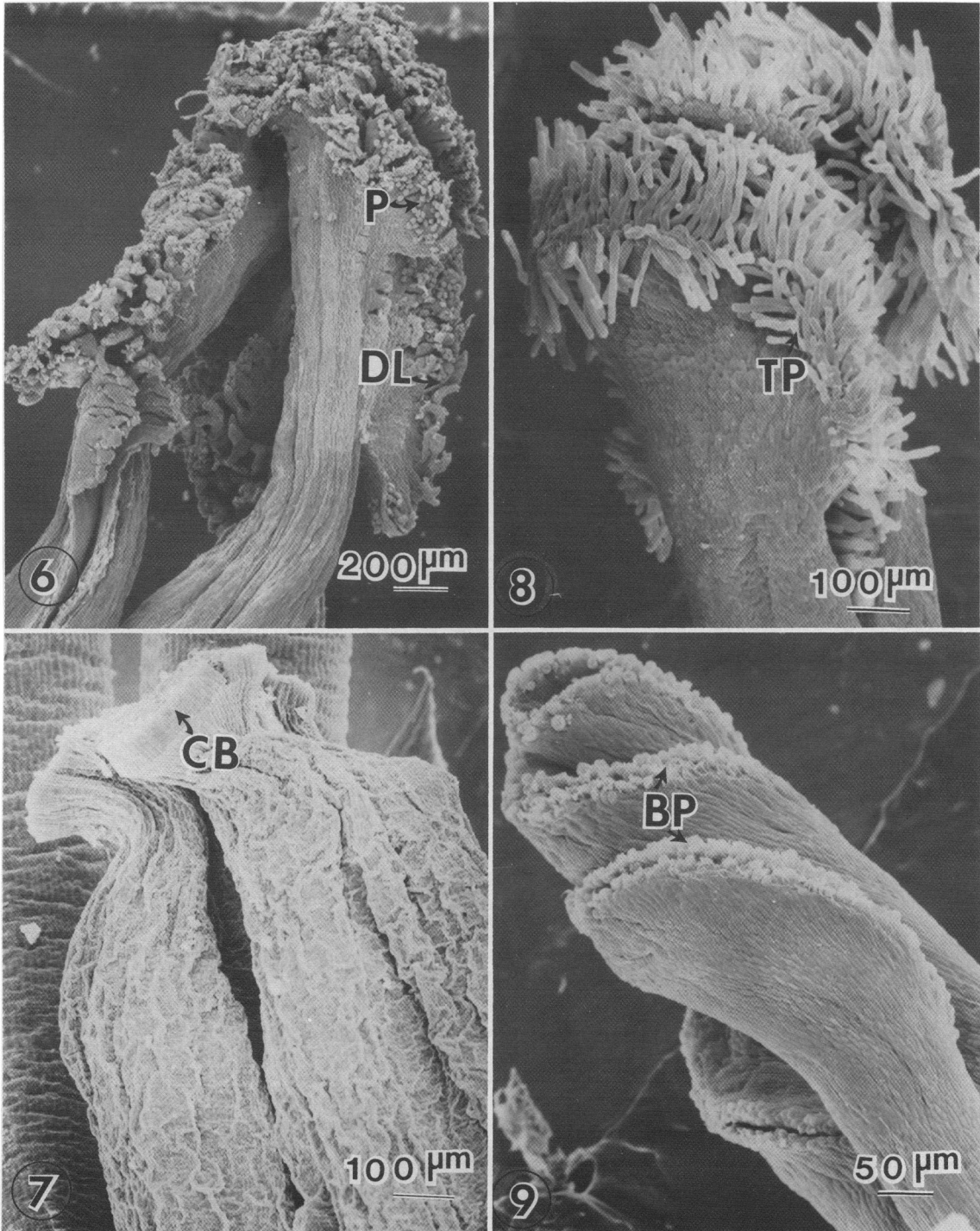
STIGMA MORPHOLOGY.—Terminology of the stigma types follows BROWN and GILMARTIN (1984). The most commonly observed stigma type in the subfamily is the conduplicate-spiral pattern, type II (figs. 1–6, 8–11). The simple-erect type I occurs

in *Brocchinia*, *Cottendorfia*, and *Fosterella*. The convolute-blade stigma, type III, previously reported only from the subfamily Tillandsioideae, occurs in *Navia* (fig. 7).

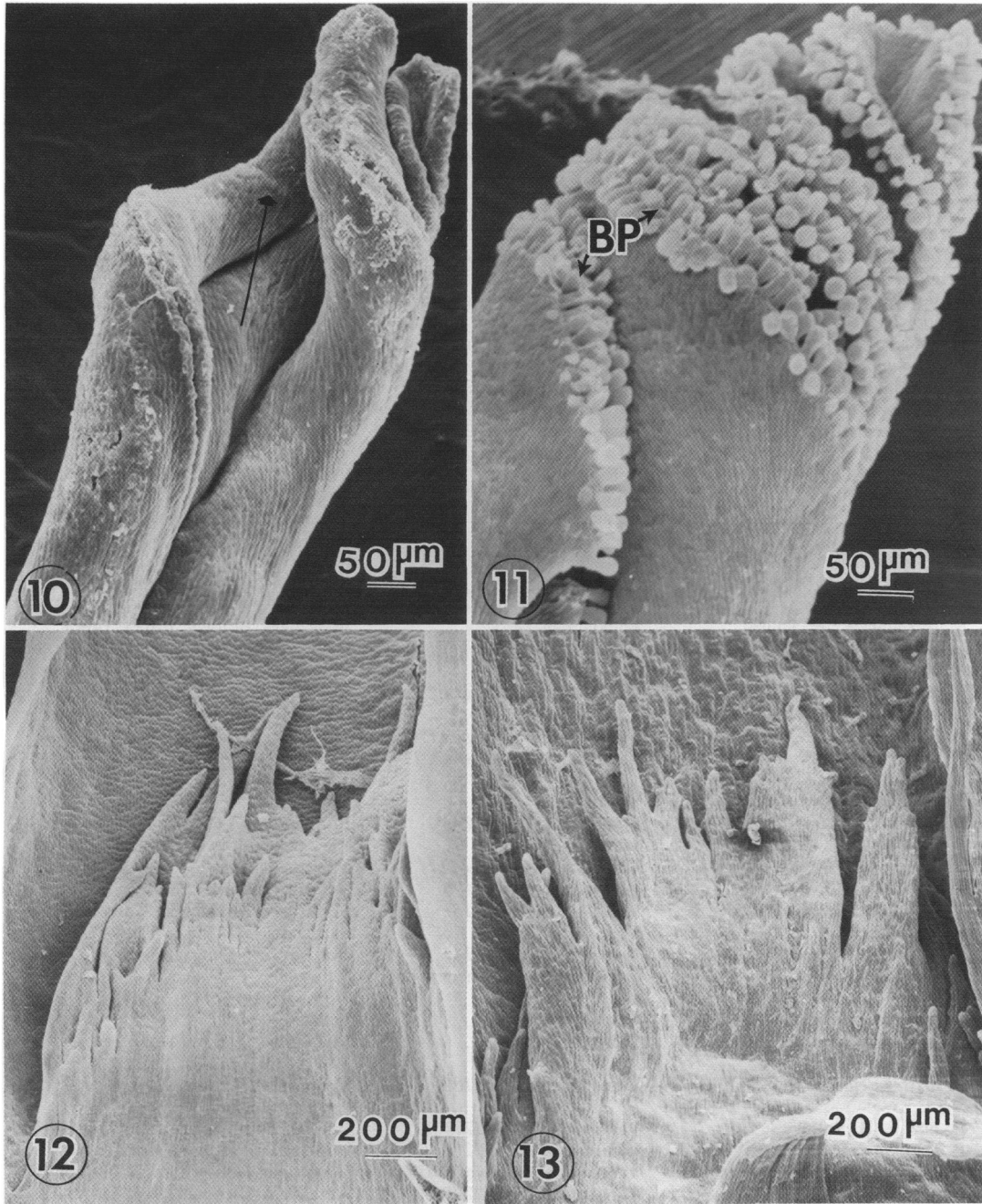
Stigma types vary within themselves as well as within certain taxa; e.g., species of *Brocchinia* exhibit types I and II (table 2). We confirm reports of a modified conduplicate-spiral type (type II) in



FIGS. 1–5.—SEM of variation in stigma morphology. Fig. 1, *Ayensua uaipanensis* (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.



FIGS. 10–13.—Figs. 10, 11, SEM of variation in stigma morphology in *Puya*. Fig. 10, *P. laxa* (SEL 83-207). A pre-anthesis type II stigma. Arrow indicates stigma lobes that begin to undergo spiraling. Papillae absent at this stage. Fig. 11, *P. harmsii* (Varadarajan et al. 1245). Type II stigma with highly compacted, spirally folded lobes at anthesis. Bulbous papillae (BP) are confined to edges of stigma lobes. Figs. 12, 13, SEM of petal scales of *Deuterocohnia*. Note the similarity of scales within the two species. Fig. 12, *D. longipetala* (Varadarajan et al. 1244). Fig. 13, *D. haumanii* (Varadarajan et al. 1250).

B. acuminata (figs. 2, 3) and of a weakly conduplicate-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 INCLUDED IN THE STUDY OF FLORAL FEATURES OF THE SUBFAMILY PITCAIRNOIDEAE

Taxa	Details of voucher	Locality
<i>Ayensua</i> :		
<i>A. uaipanensis</i> L. B. Smith ^a	Varadarajan 1196	Venezuela: Bolivar, Auyan Tepui
<i>Brocchinia</i> :		
<i>B. acuminata</i> L. B. Smith ^a	Varadarajan & Oliva 1159	Venezuela: Bolivar, La Escalera
<i>B. gilmartinii</i> Varadarajan ^a	Varadarajan & Oliva 1158	Venezuela: Bolivar, La Escalera
<i>B. steyermarkii</i> L. B. Smith ^a	Varadarajan & Oliva 1164	Venezuela: Bolivar, La Gran Sabana
<i>Cottendorfia</i> :		
<i>C. gutanensis</i> Kl. ex Bak. ^a	Varadarajan & Oliva 1161	Venezuela: Bolivar, Kavanayan
<i>Deuterocohnia</i> :		
<i>D. haumanii</i> Castell. ^a	Varadarajan et al. 1250	Argentina: Salta, Cafayate
<i>D. longipetala</i> Mez ^a	Varadarajan et al. 1244	Argentina: Cordoba, Sierra Chica
<i>D. schreiteri</i> Castell. ^a	Varadarajan et al. 1248	Argentina: Salta, Cafayate
<i>Dyckia</i> :		
<i>D. brevifolia</i> Bak. ^a	SEL 82-558 ^b	Brazil
<i>D. niederleini</i> Mez ^a	GSV 0030 ^b	Brazil
<i>D. ragonesei</i> Castell. ^a	Varadarajan 1218	Argentina: Entre Rios Rio Parana
<i>Fosterella</i> :		
<i>F. elata</i> Luther ^a	Holotype ^b	Bolivia
<i>E. penduliflora</i> L. B. Smith ^a	SEL 024397 ^b	Peru
<i>Navia</i> :		
<i>N. splendens</i> L. B. Smith ^a	Varadarajan 1215	Venezuela: Bolivar, Auyan Tepui
<i>Pitcairnia</i> :		
<i>P. andreana</i> Linden ^a	SEL 82-554 ^b	Colombia
<i>P. armata</i> Maury ^a	Varadarajan & Gaunchez 1150	Venezuela: T. F. Amazonas, P. Auyacucho
<i>P. brevicalycina</i> Mez ^a	Varadarajan & Ortega 1156	Venezuela: Trujillo, Bocono
<i>P. bulbosa</i> L. B. Smith ^a	Varadarajan & Gaunchez 1143	Venezuela: T. F. Amazonas, P. Auyacucho
<i>P. corallina</i> Linden & Andre	Varadarajan 1192	Colombia
<i>P. crassa</i> L. B. Smith	Varadarajan et al. 1292	Bolivia: Nor-Yungas
<i>P. ctenophylla</i> L. B. Smith ^a	Varadarajan 1195	Venezuela: Bolivar, Auyan Tepui
<i>P. heterophylla</i> Beer ^a	Varadarajan & Oliva 1171	Venezuela: Aragua, Pittier Natl. Park
<i>P. meridensis</i> Kl. ex Mez ^a	Varadarajan et al. 1176	Venezuela: Merida, Paramo de Colorados
<i>P. nubigena</i> Planch. & Linden	Varadarajan et al. 1181	Venezuela: Merida, La Carbonero
<i>P. nuda</i> Baker ^a	SEL 81-1979 ^b	Surinam
<i>P. paniculata</i> R. & P.	Varadarajan et al. 1281	Bolivia: Nor-Yungas, Yalosa
<i>P. pruinosa</i> H. B. K. ^a	Varadarajan & Gaunchez 1147	Venezuela: T. F. Amazonas, P. Auyacucho
<i>P. pungens</i> H. B. K.	SEL 016687 ^b	Ecuador
<i>P. punicea</i> Scheid.	SEL 80-1590 ^b	Mexico
<i>Puya</i> :		
<i>P. aristeguietae</i> L. B. Smith ^a	Varadarajan et al. 1188	Venezuela: Tachira, Paramo de Zumbador
<i>P. atra</i> L. B. Smith	Varadarajan et al. 1274	Bolivia: Sud-Yungas, Unduavi
<i>P. ferruginea</i> L. B. Smith ^b	Varadarajan et al. 1272	Bolivia: La Paz, La Florida
<i>P. floccosa</i> E. Morr. ex Mez ^a	Varadarajan & Oliva 1163	Venezuela: Bolivar, La Gran Sabana
<i>P. harmsii</i> Castell. ^a	Varadarajan et al. 1245	Argentina: Tucuman, Tafi del Valle
<i>P. laxa</i> L. B. Smith ^a	SEL 83-207 ^b	Bolivia
<i>P. lilloi</i> Castell	Varadarajan 1229	Argentina: Salta, El Tala
<i>P. mirabilis</i> L. B. Smith ^a	Varadarajan 1230	Argentina: Salta Rio Blanco
<i>P. pearcei</i> Mez	Varadarajan et al. 1286	Bolivia: Nor-Yungas, Yalosa
<i>P. stenothyrsa</i> Mez	Varadarajan & Canne 1310	Bolivia: La Paz, Sorata
<i>P. trianae</i> Bak	Varadarajan et al. 1189	Venezuela: Tachira, Paramo de Zumbador
<i>P. tristis</i> L. B. Smith ^a	Varadarajan & Canne 1306	Bolivia: Cochabamba, Tiraque

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

^a Taxa processed for SEM.^b 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) ^a
<i>Ayensua</i>	1	II
<i>Brewcaria</i>	(I ^b)
<i>Brocchinia</i>	3	I (I ^{c,d}), II (II ^{c,d})
<i>Cottendorfia</i>	1	I
<i>Deuterocohnia</i>	3	II (II ^c)
<i>Dyckia</i>	3	II (I, ^c II ^c)
<i>Encholirium</i>	(II ^c)
<i>Fosterella</i>	2	I (I ^c)
<i>Hechtia</i>	(I, ^c II ^c)
<i>Navia</i>	1	III (flabelliform [III?] ^c)
<i>Pitcairnia</i>	15	II (II ^{c,d})
<i>Puya</i>	12	II (II ^c)
<i>Steyerbromelia</i>	(II ^b)

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

^a Definition according to BROWN and GILMARTIN (1984).

^b From SMITH (1984).

^c From MEZ (1934–1935).

^d 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.

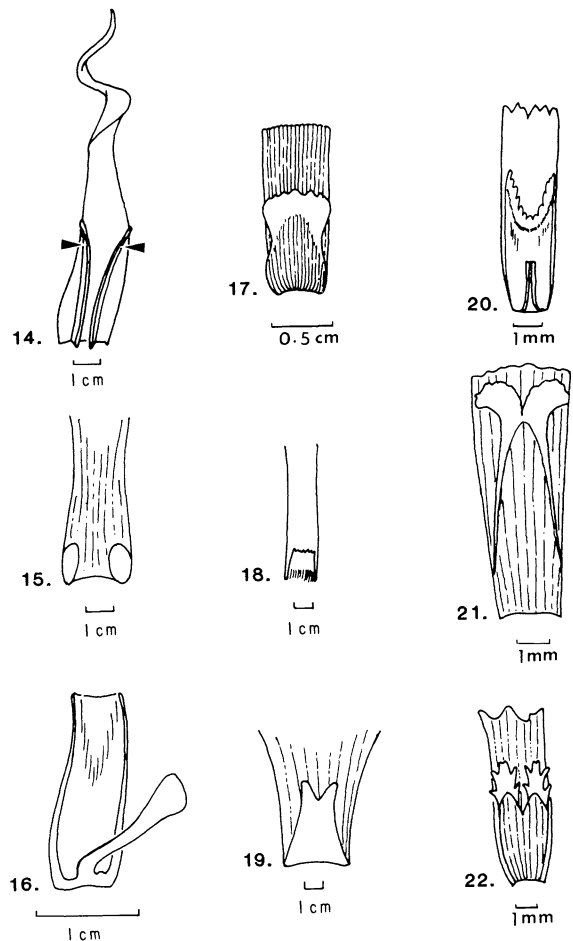
COMPACTION OF THE STIGMA BRANCHES.—Describing the degree of compaction of stigma lobes is very subjective as it depends on the size and shape of the individual lobes. Two general types of compaction of the lobes are characterized during anthesis. In the first type, the individual lobes are conduplicately 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, spatulate (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*, *Brewcaria*, and *Deuterocohnia*. Yet, they show a high degree of instability in occurrence, especially among the species and popula-

tions of several *Pitcairnia* and *Puya* species (*Pitcairnia pulverulenta* R. & P., *P. schultzei* Harms, *Puya hofstenii* 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).



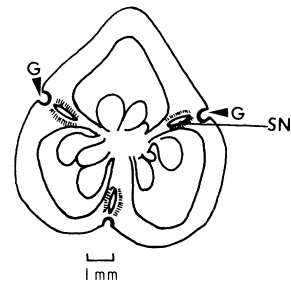
FIGS. 14–22.—Diagrams illustrating the variable morphology of petal scales. Figs. 17 and 20–22 are reproduced from SMITH and DOWNS (1974), with permission (copyright 1974, The New York Botanical Garden). Fig. 14, *Puya floccosa* (Varadarajan & Oliva 1163). Petal scales represented as vertical folds (arrows) 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 septal nectaries of Bromeliaceae correspond to the “labrynthine common nectarial cavity” type sensu SCHMID (1985). Architecture of the septal nectaries varies in superior and inferior ovaries (BUDNOWSKI 1922). Pitcairnioid flowers are uniquely suited for examining this variation as the ovaries range from fully superior to completely inferior. Septal nectaries of pitcairnioids 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 septal nectaries is lined by variable amounts of glandular tissue. Glandular tissue and the contents of the secretion of Pitcairnioideae may correspond to those of some Liliaceous members (FAHN 1949, 1952; FAHN and BENOUAICHE 1979).

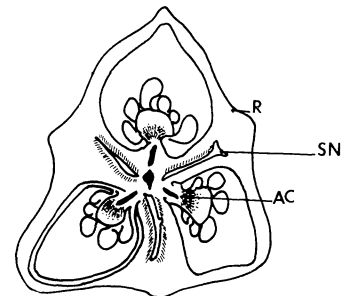
Our observations of the septal nectaries from representatives of Pitcairnioideae with superior, semi-inferior, and inferior ovaries confirm some structural variations reported by BUDNOWSKI (1922), e.g., the number of nectariferous channels, orifices. In taxa with superior ovaries (*Deuterocohnia schreiteri*, *Dyckia ragonesei*, and *Fosterella elata*), six nectariferous channels are discernible radially during the very early stages of flower development. Three channels oriented toward the septa 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*, *Cottendorfia guianensis*) and semi-inferior to inferior ovaries (*Pitcairnia heterophylla*, *Puya harmsii*, fig. 27), the nectaries include only the septal 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 septal channels (fig. 27), nectar release to the exterior by the dissolution of the septal channels seems likely. The ovary surface is mostly grooved, and the septal channels break open at the grooves (figs. 23, 28). Guided by the grooves, nectar flows from the septal channels to the ovary base, where it finally accumulates.

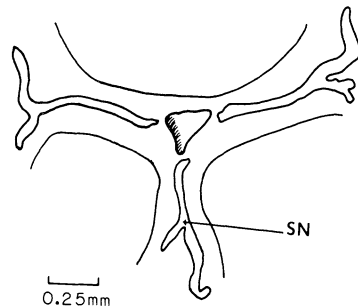
Placental channels lose their morphological identity at anthesis as they become integrated with the placental tissue. Although the actual route of nectar flow from these channels is not well understood, it appears that their secretions are partly (1)



23.



24.

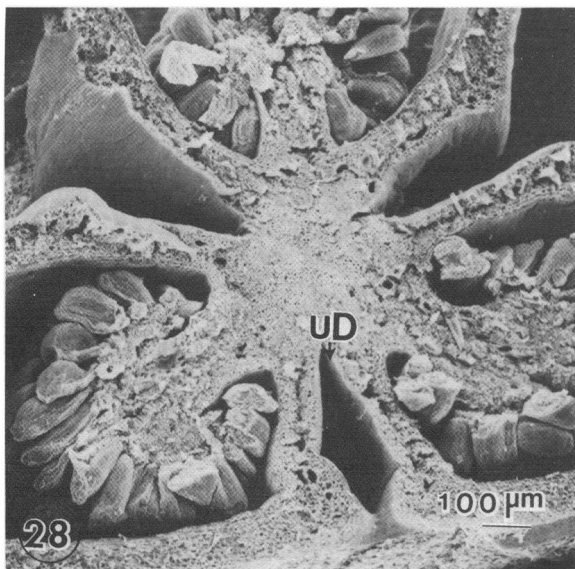
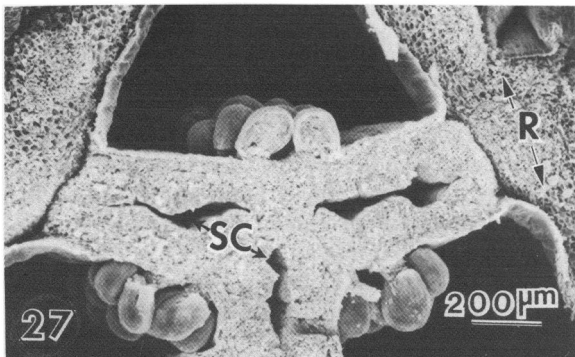
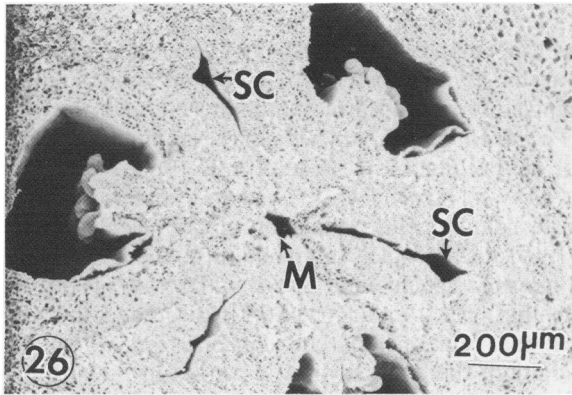


25.

FIGS. 23–25.—Cross sections of septal nectaries (SN) from pre-anthesis flowers. Fig. 23, *Puya floccosa* (Varadarajan & Oliva 1163), example of a superior ovary. G = grooves. Fig. 24, *Puya harmsii* (Varadarajan et al. 1245), semi-inferior ovary. Arrows indicate likely additional nectariferous channels (AC). Note the thick receptacular tissue (R). Fig. 25, *Navia splendens* (Varadarajan 1215) with convoluted channels of septal nectaries.

transferred into the locule via the placental tissue and (2) through the dissolved areas of the septal channels (fig. 28). From the locule, nectar flows through the apical orifices of the ovary. The dissolution of the septal channels causes the individual carpels to part from one another, leading to a superficial apocarpny (fig. 28).

Nectar release from the semi-inferior/inferior



FIGS. 26–28.—SEM of cross sections of ovaries displaying details of septal nectaries. Fig. 26, *Puya laxa* (SEL 83-207). Septal nectaries with a median channel (M) and three septal channels (SC), a typical pre-anthesis structure in most superior ovaries. Fig. 27, *Pitcairnia ctenophylla* (Varadarajan 1195). Septal channels (SC) are evident as semi-inferior/inferior ovary matures. R = receptacular tissue. Fig. 28, *Puya tristis* (Varadarajan & Canne 1306). Septal nectaries with superior ovary during anthesis. Note the dissolved areas of the channels leading to superficial apocarp. D = undissolved channel.

ovaries is slightly different from the above account. Complete epigyny 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 POLLINATION BIOLOGY

Type II stigma of Pitcairnioideae varies so widely that more than a single pollination system seems probable. The highly compact, conduplicately 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, paniced 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 septal 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, had 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 PIJL 1971; PROCTOR and YEO 1972). The pos-

sible 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*, *Brocchinia*, *Cottendorfia*, *Deuterocohnia*, *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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