Table 3.3. Distribution of palisade mesophyll in *Paphiopedilum*. None was observed in the remaining genera.

Species	Number of palisade layers present	Species	Number of palaside layers present
P. acmodontum	0-1	*P. lowii*	0
P. appletonianum	0-1	*P. mastersianum*	1
P. argus	0-1	*P. parishii*	1-2
P. bellatulum	0-2	*P. philippinense*	1-2
P. bullenianum	0-2	*P. praestans*	1-2
P. callosum	0-1	*P. purpuratum*	0-1
P. ciliolare	0-1	*P. randsii*	0-1
P. concolor	1-3	*P. rothschildianum*	0-1
P. curtisii	0-1	*P. spicerianum*	1-2
P. exul	0-1	*P. sukhakulii*	0-2
P. fairieanum	2-3	*P. tonsum*	0-1
P. haynaldianum	2	*P. victoria-regina*	
P. hennisianum	0-1	ssp. *chamberlainianum*	1
P. hirsutissimum	0-1	ssp. *liemianum*	1
P. laevigatum	1-2	ssp. *primulinum*	2-3
P. lawrenceanum	0-2	*P. violascens*	0-1

Table 3.4. Distribution of palisades in ten species of mottled-leaved *Paphiopedilum*.

Species	Number of layers over light patches	Number of layers over dark patches	Species	Number of layers over light patches	Number of layers over dark patches
P. bellatulum	0-1	2	*P. linii*	0-1	1-2
P. bullenianum	0-1	1-2	*P. purpuratum*	0	1
P. concolor	1	2-3	*P. sukhakulii*	0-1	1-2
P. curtisii	0	1	*P. tonsum*	0	1
P. lawrenceanum	0-1	1-2	*P. victoria-regina*		
			ssp. *liemianum*	1	1

Table 3.5. Distribution of unilocular and trilocular ovaries, and sinuous epidermal cells in slipper orchid perianths. Features coded in parentheses are transitional and difficult to categorize.

Species	Carpels fused to form axis			At least some epidermal cell walls sinuous
	base	middle	summit	
Cypripedium				
acaule	(-)	-	(-)	+
arietinum	(-)	-	-	+
californicum	+	-	-	(+)
candidum	-	-	-	(+)
guttatum	-	-	-	+
irapeanum	+	-	-	+
pubescens	-	-	-	(+)
reginae	-	-	-	+
Selenipedium				
chica	+	+	+	+
Phragmipedium				
boissierianum	+	+	+	-
caricinum	+	+	+	-
caudatum	+	+	+	-
longifolium	+	+	+	-
schlimii	+	+	+	-
wallisii	+	+	+	-
warscewiczianum	+	+	+	-
Paphiopedilum				
acmodontum	(-)	-	+	+
appletonianum	+	-	-	+
argus	+	-	(+)	+
barbatum	(-)	-	+	+
bullenianum	?	-	?	+
callosum	-	-	-	+
ciliolare	+	-	+	+
Paphiopedilum (Cont'd.)				
concolor	+	-	+	+
curtisii	?	-	?	+
delenatii	+	-	-	+
exul	+	-	+	+
fairieanum	-	-	+	+
godefroyae	?	-	?	+
haynaldianum	+	-	-	+
hennisianum	+	-	+	+
hirsutissimum	+	-	-	+
insigne	+	-	+	+
lawrenceanum	?	-	?	+
linii	?	-	?	+
lowii	-	-	+	+
mastersianum	+	-	+	+
niveum	+	-	-	+
parishii	-	-	-	+
philippinense	+	-	+	+
praestans	+	-	+	+
purpuratum	+	-	+	+
spicerianum	+	-	+	+
sukhakulii	(+)	-	+	+
tonsum	(+)	-	-	+
venustum	(+)	-	+	-
victoria-regina	-	-	+	+
violascens	(-)	-	(-)	+

dermal cells are initially formed, which include barrel-shaped guard cell mother cells (GMCs). One or both cells flanking the GMCs undergo unequal divisions forming one or two subsidiary cells as may the polar cells. Ultimately the GMC divides forming the young guard cells. Mature leaves of *Paphiopedilum argus* and *P. fairieanum* clearly lack subsidiary cells, a feature also observed by Solereder and Meyer for *Paphiopedilum.* Presence of subsidiary cells in *Phragmipedium* × *sedenii* supports Williams' view (1975, 1976, 1979) that subsidiary cells are general features of the Orchidaceae.

FLORAL ANATOMY

Swamy (1948) studied the vascularization of slipper orchid flowers (one *Cypripedium* and two *Paphiopedilum* species). He found that the flowers were provided with 6 vascular bundles with rather simple branching patterns. He found no support for Darwin's theory (1885) that the lip comprises one petal plus two fused lateral stamens, but neither did he find evidence against it. Rao (1974) found a similar vascular anatomy in the Apostasioideae, which he believed is evidence for relationship with the Cypripedioideae.

Ovary anatomy has been stressed as fundamentally important in defining genera (Reichenbach, 1854; Pfitzer, 1903; Rolfe, 1896). When sectioned through the midregions *Cypripedium* and *Paphiopedilum* have unilocular ovaries with parietal placentas. The distinction was first recognized when Reichenbach (1854) erected *Selenipedium* for those species with trilocular ovaries, leaving others with unilocular ovaries in *Cypripedium.* Blume (1858) questioned this distinction since he noted that the ends of the seed chamber may be trilocular. Pfitzer (1903) further emphasized midovary placentation in generic recognition, as has Brieger (1971).

Newton and Williams (1978) examined pollen morphology from 1 *Selenipedium*, 7 *Cypripedium*, 6 *Phragmipedium* and 27 *Paphiopedilum* species. The few differences observed were essentially as great between closely allied species as among genera.

Gametogenesis has been reviewed most recently by Davis (1966) and Abe (1972). Embryo sac development is of the *Allium* type, but occasionally a cell division is arrested, i.e., "strike" occurs.

Additional Anatomical Evidence. Since locule number is considered fundamentally important in distinguishing genera, a study was undertaken to determine if emphasis on this singular feature is justified. A second study on the distribution of sinuous anticlinal walls in epidermal cells of perianths is also presented.

Ovary placentation was studied in 8 species of *Cypripedium*, 1 *Selenipedium*, 4 *Phragmipedium*, and 23 *Paphiopedilum* species. Hand sections were prepared from the base, middle, and summit portions of ovaries stored in 50% FPA (5 parts formalin, 5 parts propionic acid, and 90 parts 50% ethanol). Presence of sinuous anticlinal walls of epidermal cells was studied in 1 *Selenipedium*, 9 *Cypripedium*, 7 *Phragmipedium*, and 33 *Paphiopedilum* species. The epidermal cells of perianths were prepared by simply cutting sections of a perianth tissue preserved in FPA, and mounting in 50% ethanol under a cover slip.

The results of the ovary study are summarized in Table 3.5. As noted by Reichenbach (1854), Rolfe (1896), and Pfitzer (1903), the mid-sections exhibit 3 locules in *Selenipedium chica* (Fig. 3.6A) and *Phragmipedium longifolium* (Fig. 3.6B). The carpels of *S. chica* are not swollen in immature ova-

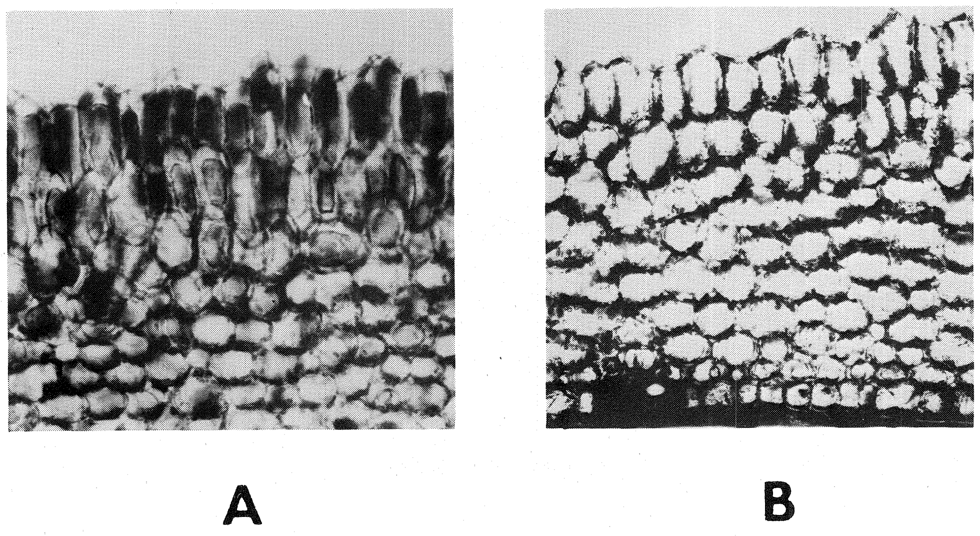

Fig. 3.2 Hand sections through mottled leaves of *Paphiopedilum concolor.* A. A dark-appearing section of leaf tissue with two distinct layers of palisades (X 30). B. A light-appearing section of leaf tissue with only one layer of palisades centrally (X 30).

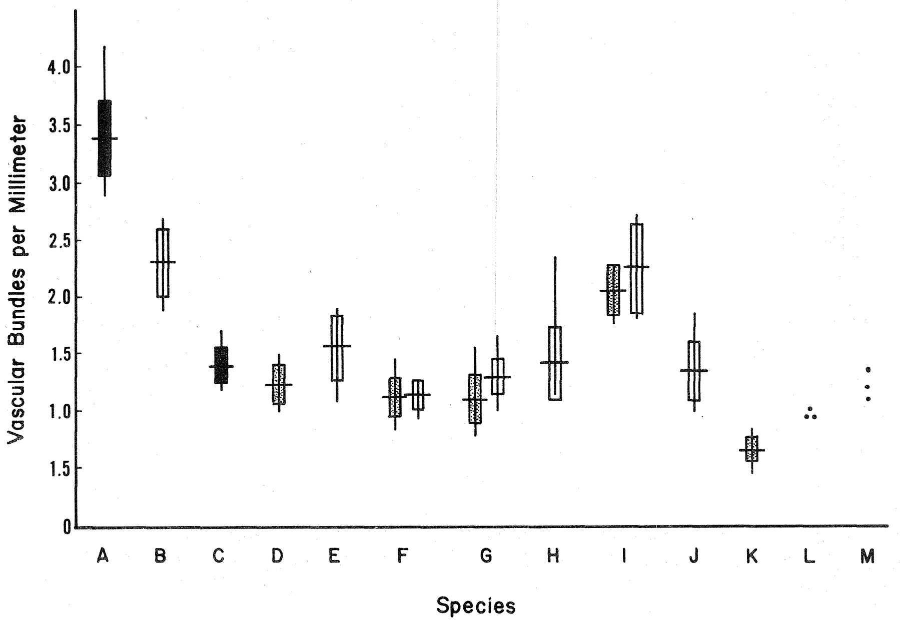

Fig. 3.3. Spacing of vascular bundles in 13 plicate-leaved species. Ranges, means, and standard deviations are given where leaves number more than five per sample. As expected, samples taken from herbarium specimens (unshaded rectangles) generally exhibit closer spacing than fresh material (stippled). Solid rectangles represent samples taken from specimens preserved in FPA. A. *Selenipedium chica.* B. *Cypripedium irapeanum.* C. *C. californicum.* D. *C. arietinum.* E. *C. passerinum.* F. *C. reginae.* G. *C. pubescens.* H. *C. parviflorum.* I. *C. candidum.* J. *C. montanum.* K. *C. acaule.* L. *C. formosanum* (herbarium specimen). M. *C. guttatum* (preserved in FPA).

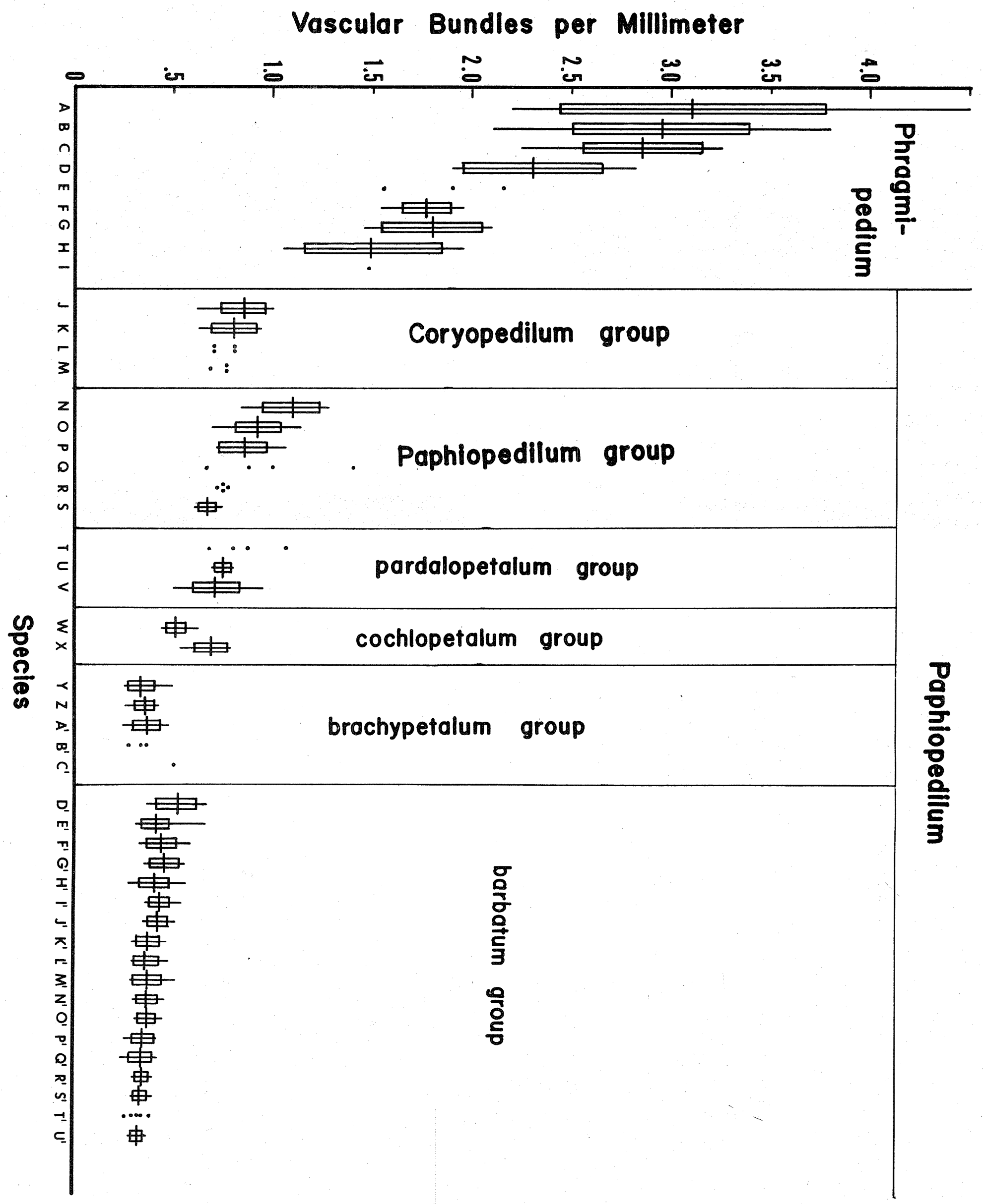

Fig. 3.4. Spacing of vascular bundles in 45 conduplicate-leaved species. Each histogram represents the range, mean, and standard deviation per species sampled. Samples with five or fewer measurements are represented as points. The species are approximately arranged according to decreasing density of vascular bundles within natural species groups. A. *Phragmipedium longifolium* entity *gracile*. B. *P. caricinum*. C. *P. pearcei*, D. *P. boissierianum*. E. *P. schlimii*. F. *P. longifolium* subsp. *longifolium*. G. *P. wallisii*. H. *P. warscewiczianum*. I. *P. caudatum*. J. *Paphiopedilum praestans*. K. *P. philippinense*. L. *P. rothschildianum*. M. *P. stonei*. N. *P. insigne*. O. *P. fairieanum*. P. *P. hirsutissimum*. Q. *P. exul*. R. *P. villosum*. S. *P. spicerianum*. T. *P. haynaldianum*. U. *P. lowii*. V. *P. parishii*. W. *P. victoria-regina* subsp. *liemianum*. X. *P. victoria-regina* subsp. *primulinum*. Y. *P. bellatulum*. Z. *P. concolor*. A'. *P. niveum*. B'. *P. delenatii*. C'. *P. godefroyae*. D'. *P. lawrenceanum*. E'. *P. mastersianum*. F'. *P. appletonianum*. G'. *P. ciliolare*. H'. *P. venustum*. I'. *P. argus*. J'. *P. barbatum*. K'. *P. tonsum*. L'. *P. violascens*. M'. *P. acmodontum*. N'. *P. sukhakulii*. O'. *P. bullenianum*. P'. *P. callosum*. Q'. *P. curtisii*. R'. *P. hennisianum*. S'. *P. purpuratum*. T'. *P. celebesense*. U'. *P. linii*.

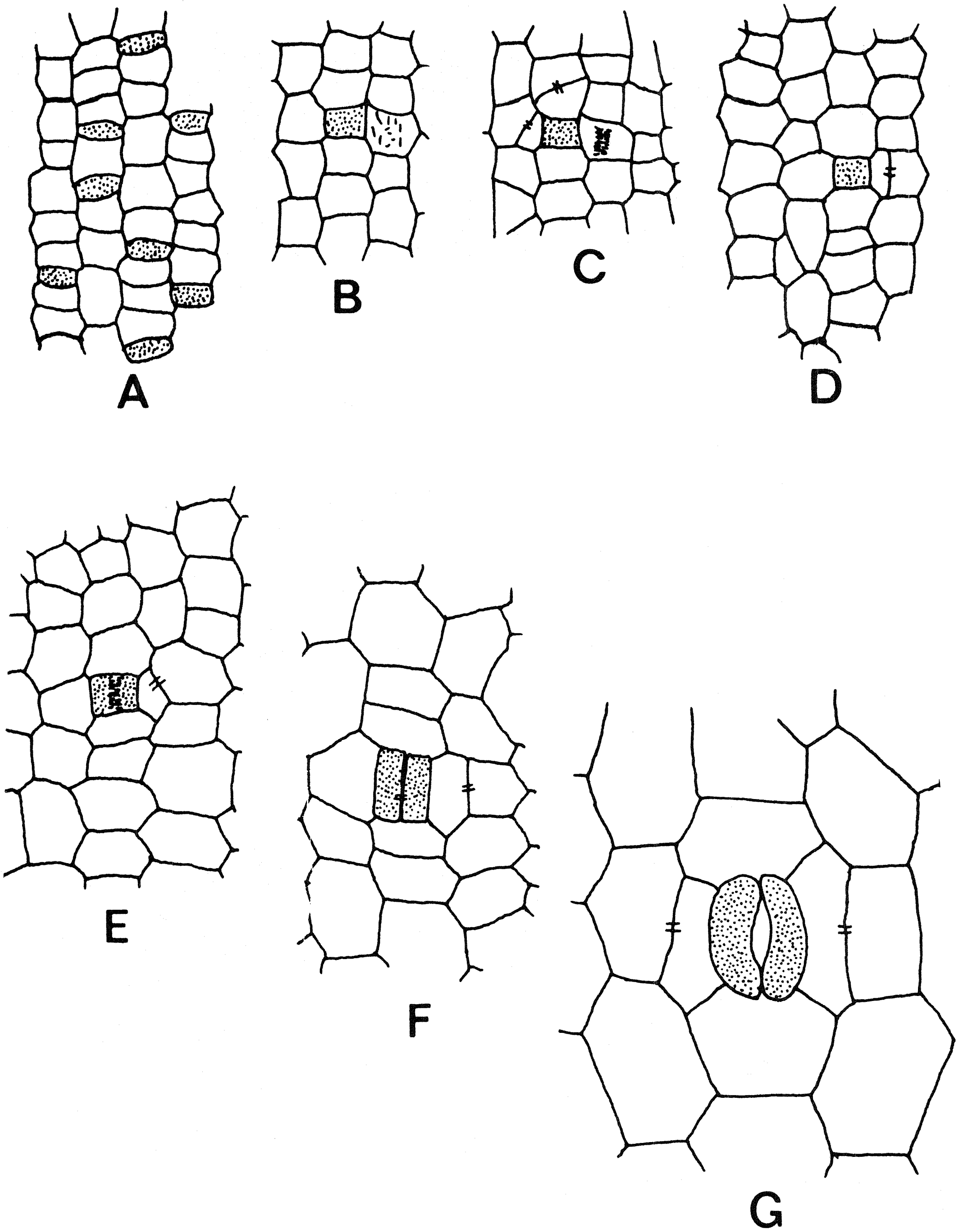

Fig. 3.5. Stomatal development in *Phragmipedium* X *sedenii* . Stippled cells are guard cells or guard cell mother cells (GMCs). A pair of tick marks indicate cell walls which segregated subsidiary cells. The scale line is 0.2 mm. A. Flanks of cells with barrel-shaped GMCs. B. One of the lateral epidermal cells in prophase. C. GMC with at least two subsidiary cells and a cell division at metaphase, which is expected to form another subsidiary cell. D. GMC with one, possibly two subsidiary cells. E. GMC at metaphase. F. Immature guard cells immediately following cell division. G. Mature stomate with two lateral subsidiary cells. The terminal or polar cells are probably subsidiary also.

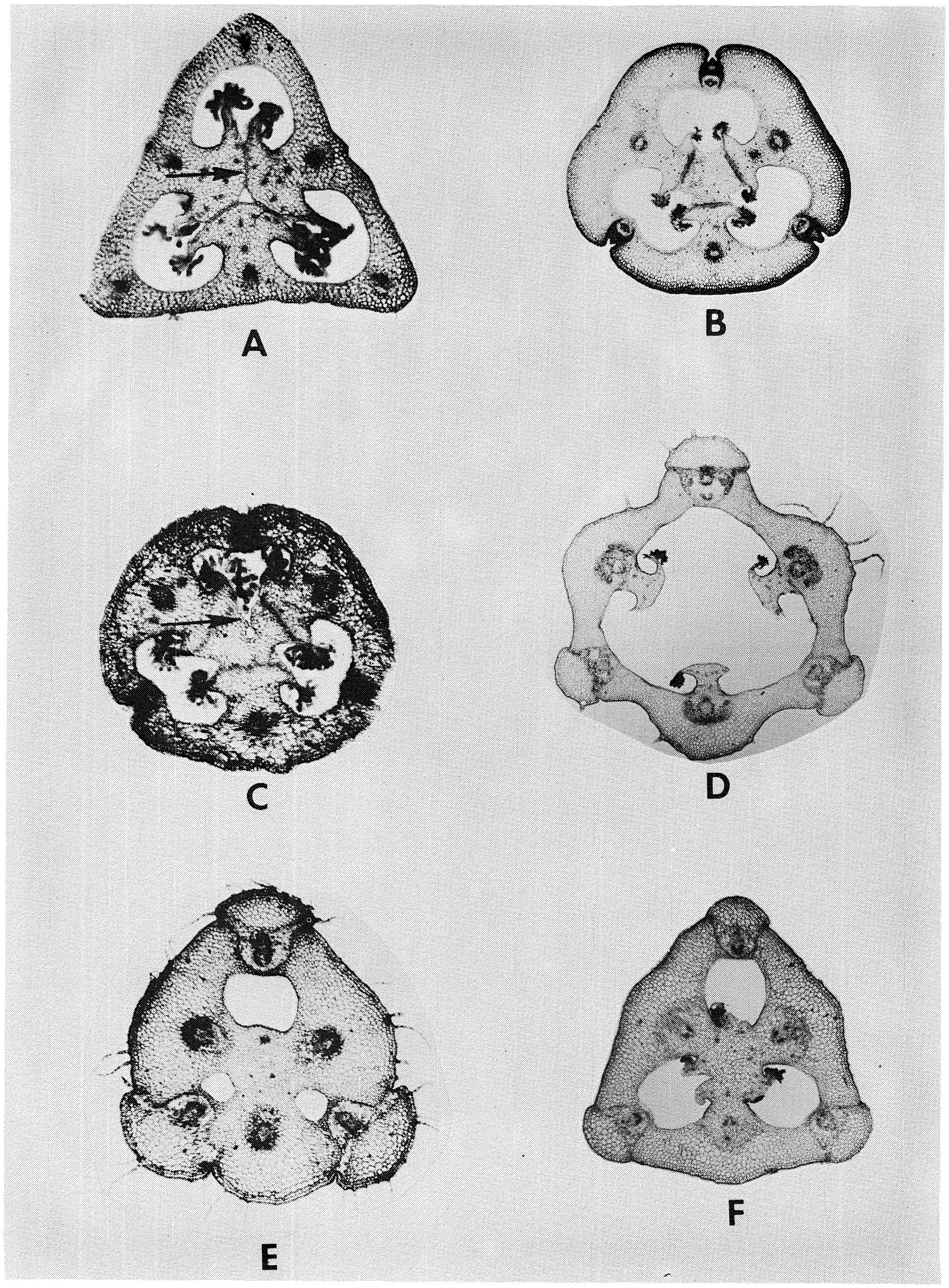

Fig. 3.6. Ovary anatomy in the Cypripedioideae. A. *Selenipedium chica* showing axile placentation. Note the sutures outlined by enlarged cells which resemble epidermal cells (X 23). B. *Phragmipedium longifolium* with axile placentation, but the central region contains a pith (X 36). C. *Phragmipedium schlimii* with axile placentation similar to that of *P. longifolium*, but note the central separation, which may represent a critical step toward parietal placentation (X 18). D. Midsection of *Paphiopedilum mastersianum* ovary showing characteristic parietal placentation (X 6.8). E. Basal section of *Paphiopedilum hennisianum* with an axis and three locules (X 11). F. Ovary base of *Paphiopedilum mastersianum* showing axis with three locules (X 12).

Table 3.6. Geographic distribution of leaf patterning in *Paphiopedilum* Section *Barbata*. Contrast in mottling was judged according to a three point system: Weak (W), Intermediate (I), and Strong (S).

Mainland Southeast Asia	
P. appletonianum	W-I
P. barbatum	I
P. callosum	W-S
P. johorensis	I
P. purpuratum	I-S
P. robinsonii	I
P. sukhakulii	I-S
P. venustum	S
P. wardii	S

Borneo and Celebes	
P. amabile	S
P. bullenianum	S
P. celebesense	S
P. dayanum	S
P. hookerae	S
P. lawrenceanum	S
P. linii	S
P. virens	I-S

Java and Sumatra	
P. curtisii	S
P. javanicum	S
P. superbiens	S
P. tonsum	S

Philippines	
P. acmodontum	I
P. argus	I
P. ciliolare	W
P. hennisianum	W

New Guinea and adjacent islands	
P. bougainvilleanum	W
P. mastersianum	W-I
P. papuanum	I?
P. violascens	W
P. wentworthianum	W

Table 3.7. Generic summary of grazing and browsing mammals within range of _Paphiopedilum_ Section _Barbata_. An asterisk (*) indicates genera of widespread occurrence and probable importance to terrestrial plants. Introduced genera are excluded where possible.

ORDER	FAMILY	GENUS	GEOGRAPHIC REGION						
			Mainland SE Asia	Sumatra	Java	Borneo	Celebes and nearby isls.	Philippines	New Guinea (plus Bismarcks)
Artiodactyla	Bovidae	_Anoa_	-	-	-	-	+	Mindoro only	-
"	"	_Bos_	+	-	+	-	-	-	-
"	"	_Bubalus_*	+	+	+	+	+	-	-
"	"	_Capricornis_	+	+	-	-	-	-	-
"	"	_Hemitragus_	+	-	-	-	-	-	-
"	"	_Naemorhedus_	+	-	-	-	-	-	-
"	Cervidae	_Axis_	+	-	-	-	-	Calamian Isls.	-
"	"	_Capreolus_	+	-	-	-	-	-	-
"	"	_Cervus_*	+	+	+	+	+	+	-
"	"	_Elaphodus_	+	-	-	-	-	-	-
"	"	_Muntiacus_*	+	+	+	+	+	-	-
"	Suidae	_Babyrousa_	-	-	-	-	+	-	-
"	"	_Sus_*	+	+	+	+	+	-	-
"	Tragulidae	_Tragulus_*	+	+	+	+	+	SW only	-
Lagomorpha	Ochotonidae	_Lepus_	+	-	-	-	-	-	-
"	"	_Nesolagus_	-	+	-	-	-	-	-
Marsupialia	Macropodidae	_Thylogale_	-	-	-	-	-	-	+
"	"	_Wallabia_	-	-	-	-	-	-	+
Perissodactyla	Equidae	_Equus_	(+?)	-	-	-	-	-	-
"	Rhinocerotidae	_Didermocerus_	+	+	-	+	-	-	-
"	"	_Rhinoceros_	+	+	+	-	-	-	-
"	Tapiridae	_Tapirus_	+	+	-	-	-	-	-
Proboscidea	Elephantidae	_Elephas_	+	+	-	+	-	-	-
	Total Genera:		17-18	11	7	7	7	4	2

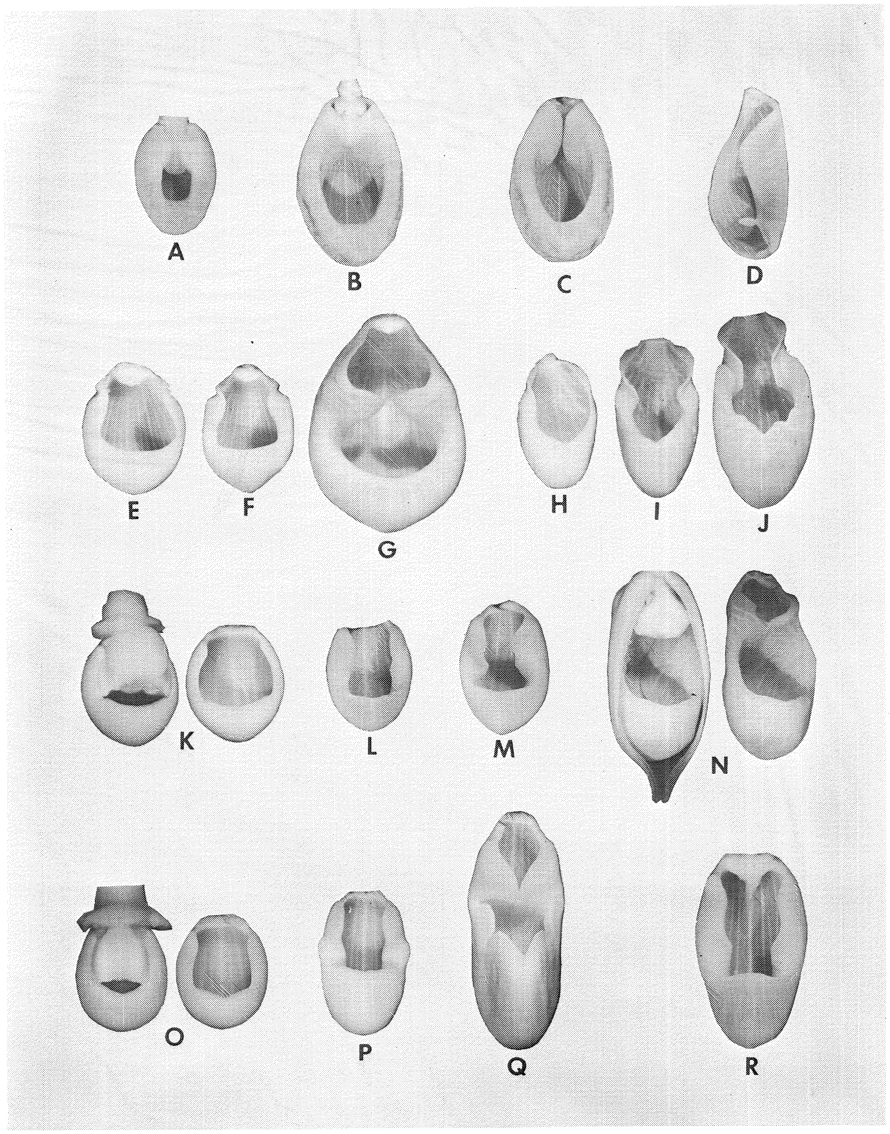

Fig. 3.7. Developing labella arranged sequentially. A-D. *Selenipedium chica.* A. Immature lip with staminode (X 3.6). B. Lip just before anthesis showing the greater enlargement of the lip relative to the staminode (X 2.1). C. Same as B but without staminode (X 2.1). D. Interior view of a mature lateral lobe with one-half of the lip removed (X 2.1). E-G. *Cypripedium reginae.* E. Youngest lip with initiating pair of lateral lobes (X 3.1). F. Slightly later stage showing greater development of lateral lobes (X 2.0). G. Essentially mature lip just prior to anthesis with only one pair of lateral lobes (X1.3). H-J. *Cypripedium pubescens.* H. Young lip with developing lateral lobes (X 2.1). I. Lateral lobes outturned basally where they contact the gynostemium (X 2.0). J. Lip just prior to anthesis showing moderate outpocketing near the base. Only a single pair of lateral lobes is evident (X 1.3). K-N. *Phragmipedium caricinum.* K. Lip with and without gynostemium in youngest stage. The gynostemium fills the lip, which has small lateral lobes at the base (X 6.4). L. A later developmental stage showing development of a pair of anterior lobes (X 3.2). M. Lateral lobes further enlarged (X 3.2). N. Floral bud just prior to anthesis with sepals removed (left), and the lip (right) (X 1.4). O-Q. *Phragmipedium longifolium.* O. Young lip with and without gynostemium (X 8). P. Later stage showing anterior lobes with corresponding outpocketing (X 2.9). Q. Lip just prior to anthesis with fused lateral lobes and well-developed horns (X 2.0). R. Developing lip of *Phragmipedium warscewiczianum* showing lateral lobes (X 3.1).

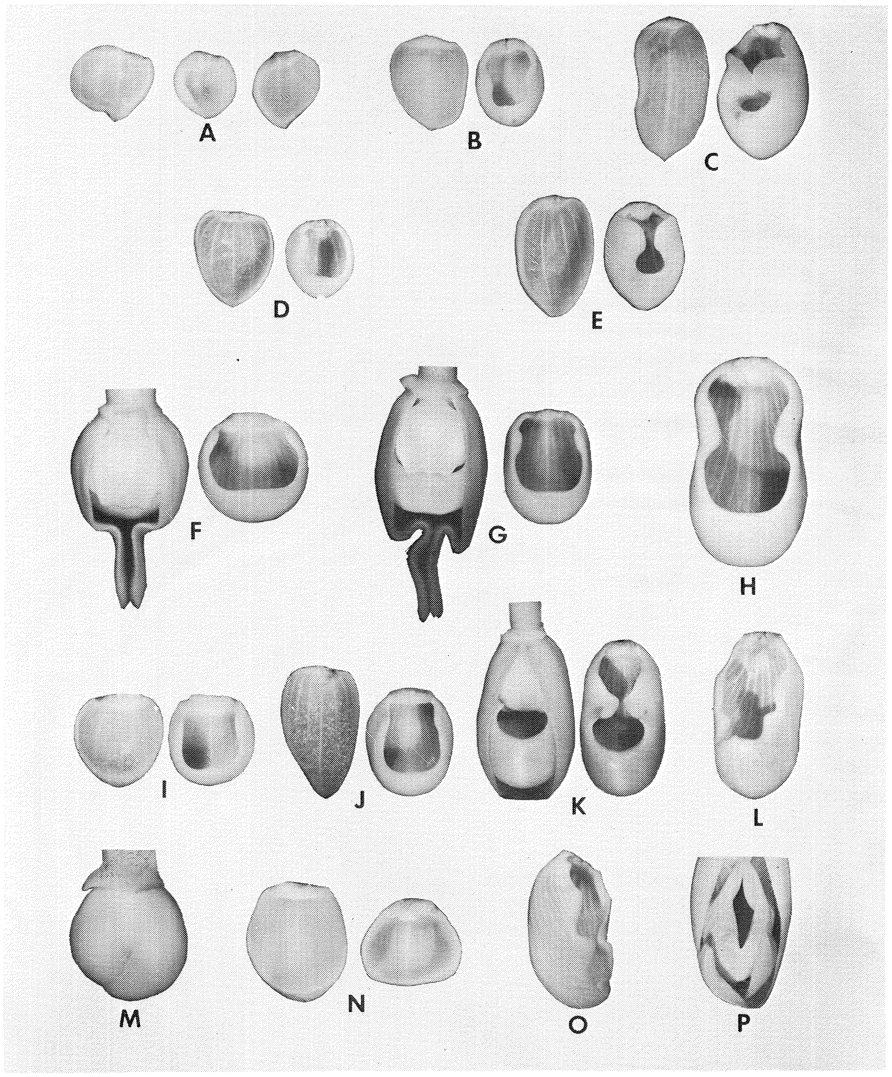

Fig. 3.8. Developing labella arranged sequentially. A-C. *Phragmipedium schlimii.* A. Lip (center) and lateral petals. The lip is relatively undifferentiated (X 16). B. Later stage of the lip (right) showing a pair of lateral lobes, and orbicular lateral petals (left) (X 3.8). C. Just prior to anthesis the lateral lobes may fuse. Lateral petal (left) is slightly elongated (X 2.2). D-E. *Paphiopedilum niveum.* D. Young lip with one pair of lateral lobes which are becoming inturned (X 3.4). E. At a later stage the lateral petals (left) are slightly elongated, and the lip (right) lacks anterior lateral lobes (X 2.5). F-H. *Paphiopedilum philippinense.* F. Bud with sepals removed showing folded lateral petals and gynostemium (left) and lip (right) with lateral lobes initiating (X 4.8). G. Slightly later stage with lateral petals more folded as they elongate (left), and lip (right) with more developed lateral lobes (X 3.0). H. Later stage, but anterior lobes are not yet present (X 3.0). In the mature flower (not shown) the anterior lateral lobes are barely apparent. I-K. *Paphiopedilum victoria-regina* subsp. *chamberlainianum.* I. The lip (right) appears similar to those of the other genera in the earliest stages. The lateral petal (left) is orbicular (X 11). J. Lip (right) is somewhat enlarged and the lateral petal (left) is elongated (X 4.7). K. Anterior lobes of the lip are formed, but unlike *Phragmipedium* turn upward (X 2.0). L. *Paphiopedilum argus.* Developing bud with anterior lateral lobes turning upward as in K (X2.5). M-P. *Paphiopedilum lowii.* M. Young bud showing vernation of orbicular petals (X 4.7). N. Lateral petal (left) and undifferentiated lip (right) lacking lateral lobes (X 4.7). O. Lip with anterior lobes turning upward (X2.4). P. Lip and lateral petals in bud just prior to anthesis showing conspicuous auricles, which developed from the anterior lobes (X 1.3).

ries as otherwise indicated by the drawing of Reichenbach (1854) and so often reproduced (Pfitzer, 1903; Garay, 1960; Brieger, 1971). Apparently Reichenbach was depicting a mature capsule as ovaries sampled at anthesis appear indistinguishable from those of *S. isabelianum* (Pfitzer, 1903). In *S. chica* the three placentas have enlarged epidermal cells where adjacent carpel walls come into contact. *Phragmipedium* appears similar to *Selenipedium*, but parenchyma tissue occurs in the central region, and the epidermal cells are not distinctive. One transverse section of *P. schlimii* shows incomplete fusion between two adjacent carpels (Fig. 3.6C) suggesting an initial step in the evolution of parietal placentation.

In *Cypripedium* and *Paphiopedilum* (Fig. 3.6D) the ovaries are always unilocular in mid-section, and the placentas are parietal. However, as noted by Blume (1858), placental fusion may occur at the ends of the seed chamber (Fig. 3.6E, F). In *Cypripedium* placental fusion with formation of two or more locules was apparent only in basal sections of *C. californicum* and *C. irapeanum*. In *Paphiopedilum* placental fusion was exhibited in either basal or summit sections, sometimes in both. Although the unilocular and trilocular conditions appear strikingly different in mid-sections, these studies show that intermediate conditions exist. The emphasis on differences in locule number based on mid-sections is not justified. This is not a surprising conclusion, as similar situations are known in other families, e.g., the Tiliaceae (Weibel, 1945).

The results of the perianth epidermal cell study are summarized in Table 3.5 In all plicate-leaved species studied, the anticlinal walls are sinuous and appear similar to leaf epidermal cells. No sinuous anticlinal walls were observed in *Phragmipedium.* In *Paphiopedilum* sinuous margins were observed only on or near the margins of the perianth parts. Only in *P. venustum* were sinuous anticlinal walls absent.

SPECULATED FUNCTIONS OF ANATOMICAL FEATURES

Several anatomical features in the slipper orchids probably represent adaptations to environmental conditions. Within temperate *Cypripedium* the roots lack a velamen, exodermis, and multiseriate pericycle, the stems lack an endodermis, and the leaves lack an endodermis. Perhaps the lack of these structures provides a more open system for translocation of water and nutrients in geographic regions where shoot elongation during spring is rapid. If the lack of a "filter" system provided by velamen and endodermis should cause salt accumulation in the shoot by late summer, the ultimate death of the shoot with onset of winter would lessen the requirement for such a filter. Furthermore, the suberization of endodermal tissue would be expected to have a negative effect on the plant's energy budget; an expensive frivolity if not required in ephemeral shoots. The presence of a velamen, exodermis, and multiseriate pericycle in roots plus presence of endodermal cells in leaves of *Selenipedium*, *Cypripedium irapeanum*, and the conduplicate-leaved genera suggest that these features and less ephemeral shoots are advantageous in the tropical species.

The micropapillose and rugose epidermal cells of *Paphiopedilum* subgenus *Barbata* (and perhaps *Phragmipedium schlimii*) may be adaptations for capture of light directed at oblique angles to the leaf. This would be advantageous to the barbatas inhabiting forest floor environments, where light levels are low and diffuse (Atwood & Williams, 1979). However, the presence of *Phragmipedium schlimii* in open habitats (C. H. Dodson, personal communication) casts some doubt upon this function. Clearly a field-oriented as well as laboratory experimental approach is necessary to elucidate the role of epidermal cell sculpturing.

The mottled leaf and associated unequal distribution of palisades in *Paphiopedilum* subgenus *Barbata* may serve as camouflage or make the plants possessing them appear unpalatable through some unknown kind of mimicry. There appears to be essentially no significance of leaf patterning to species concepts as *Paphiopedilum callosum* and *P. sukhakulii* exhibit a broad range of leaf patterns. Furthermore, species apparently closely related on the basis of floral morphology such as *P. bullenianum* and *P. appletonianum* exhibit very diverse leaf patterns. Despite the lack of taxonomic significance, there is a distinct geographic component to leaf patterning (see Table 3.6). If one evaluates the leaves on a three point scale (weak, intermediate, strong), we see that almost all plants originating from Java, Sumatra, Borneo, and Celebes have strongly tesselated leaves whereas those from the Philippines and New Guinea exhibit consistently weak patterns. Mainland Southeast Asian species exhibit mostly intermediate to strong patterning although some are weak. If one considers the kinds of terrestrial herbivores which may consume *Paphiopedilum*, the grazers and browsers (essentially all of which are mammals) seem the most likely candidates. It is doubtful that insects are responsible for natural selection for leaf patterns because their flight capabilities bring into question why the epiphytic and cliff-inhabiting plants lack mottled leaves. Table 3.7 includes all genera of mammals which could feasibly fill such a niche, plus their geographic distributions (data from Walker et al. 1975). The mainland Southeast Asian area has 17-18 genera; Sumatra has 11; and Java, Borneo, and Celebes each have 7. New Guinea has possibly only two genera of marsupials which seem likely to behave as grazers or browsers, and the island lacks artiodactyls and perissodactyls which one normally associates with the grazing and browsing niche. The Philippines have 4 native genera, but these are mostly narrowly distributed, and it is unclear which of them occur sympatrically with terrestrial species of *Paphiopedilum.* The lack of grazing and browsing mammals on the Philippines and New Guinea correlates well with weaker leaf patterns in *Paphiopedilum* while the greater mammal diversity in the region including Borneo to Celebes correlates with stronger leaf patterns. However, the geographic correlation of leaf patterning with grazing or browsing mammals is not apparent on mainland Southeast Asia. Also *Paphiopedilum* subgenus *Brachypetalum* and *P. victoria-regina* subsp. *liemianum* often occur on cliffs, so unless they are accesible to herbivorous mammals, the significance of their mottled leaves (although appearing different from those of *P.* subgenus *Barbata*) is not apparent.

The fewer vascular bundles of *Paphiopedilum* subgenus *Barbata* compared to the non-tesselated species may be related to a lesser need for efficient and rapid translocation in the relatively moist environment of forest floors. Although *P.* subgenus *Brachypetalum* often occurs in exposed situations, the presence of enlarged water storage epidermal cells may suffice during periods of drought. In *Phragmipedium* the close vascular bundles of *P. longifolium* entity *gracile*, *P. caricinum*, and *P. pearcei* probably provide support to the wiry-textured, narrow leaves for withstanding flash floods (Atwood & Dressler, in prep.). In *Cypripedium* vascular bundles are generally more sparse than in *Selenipedium*, a condition which may be adaptive to their more ephemeral leaves. However, close spacing in *C. candidum* suggests a need for greater translocation and/or physical support in open, windy prairies.

DEVELOPMENT OF FLORAL BUDS

When observing mature flowers of very different taxa, determining the structural homologies of the floral features, especially of the labella, is problematic. In order to determine the nature of the observed differences in mature labella a developmental study of flower buds of several slipper orchids is presented here. Lesser emphasis is placed on development of petals and staminodes.

The available taxa studied include *Selenipedium chica*, *Cypripedium pubescens*, *C. reginae*, *Phragmipedium caricinum*, *P. caudatum*, *P. longifolium*, *P. schlimii*, *Paphiopedilum argus*, *P. lowii*, *P. niveum*, *P. philippinense*, and *P. victoria-regina*. Buds at various developmental stages were collected and preserved in 50% FPA. Since the timing of the bud stage from initiation is impossible to determine without destroying the inflorescence, buds were serially arranged according to increasing labellum size for determining the sequence of events. The specimens were submerged under 80% ethanol and photographed under a Wild M5 binocular dissecting microscope (see Fig. 3.7 and 3.8).

In the youngest developmental stages of diverse taxa (*Phragmipedium caricinum*, *P. schlimii*, *Paphiopedilum lowii*, and *P. niveum*) the lateral petals are orbicular or oval and lack ornamentation. Elongation occurs in later stages, and development of warts and spiraling or crisping of petal margins occurs only at beginning of anthesis. Vernation of elongate petals varies among *Cypripedium*, *Phragmipedium*, and *Paphiopedilum*. In *Cypripedium pubescens* the perforate sepal vernation allows for the development of the petals outside the bud before anthesis. In *Phragmipedium caricinum* (Fig. 3.7N), *P. caudatum*, and *P. longifolium* the lateral petals lie along single lines on each side of the labellum and initiate elongation outside the calyx only at beginning of anthesis. In *Paphiopedilum philippinense* (Fig. 3.8F, G) and *P. praestans* the petals are folded in bud so that some elongation occurs before anthesis. In *Phragmipedium schlimii* (Fig. 3.8A-C) and *Paphiopedilum* subgenus *Brachypetalum*, the petals remain broad as in the earlier bud stages.

The labellum appears similar to the petals in the youngest available stages (*Phragmipedium caricinum; P. schlimii*, Fig. 3.8A; and *Paphiopedilum lowii*, Fig. 3.8N). It lacks lobing or other ornamentation, and there is no orifice or complex margin. In slightly later stages the labellum margin is appressed to the relatively large androecium but is not infolded. In subsequent stages the labellum grows faster than the androecium, and a pair of lateral lobes develop near the base. The basal lobes and margin later become inturned. In *Selenipedium chica* (Fig. 3.7B-D) and *Cypripedium reginae* (Fig. 3.7G) the labella do not acquire any greater complexity beyond this stage, and the simple mature lips of *Cypripedium californicum*, *C. irapeanum*, and *C. arietinum* suggest similar patterns of development. *Cypripedium pubescens* (Fig. 3.7H-I) develops outpocketing at the orifice in the final stages, but the lips are otherwise similar to those of the other plicate-leaved species.

Further complexities occur in the conduplicate-leaved genera. As the labellum enlarges in *Phragmipedium caricinum* and *P. longifolium*, tissue regions anterior to the basal lobes enlarge (Fig. 3.7L, M, P) forming a pair of secondary lobes and outpockets. The outpocketing is most developed in *P. longifolium* (Fig. 3.7Q) and appears as "horns" in the mature labellum. As with the plicate-leaved genera, the margin turns inward, but both pairs of lateral lobes enlarge until they ultimately become contiguous and "fused" in the mature labellum. *Phragmipedium caudatum* also produces the extra pair of anterior lobes, and the basal margins are fused in the mature labellum. Anterior lobes were not observed in the available buds of *P. schlimii* (Fig. 3.8A-C). The auricled species of *Paphiopedilum* also develop a pair of anterior lateral lobes (see *P. victoria-regina*, Fig. 3.8I-K; *P. argus*, Fig. 3.8 L; and *P. lowii*, Fig. 3.8N-P), but they develop differently than in *Phragmipedium.* The anterior lateral lobes enlarge and turn upward as does the apical margin. As the lobes continue to enlarge, they become exaggerated into the familiar auricles. *Paphiopedilum phillippinense* (Fig. 3.8H) lacks a marked enlargement of lateral lobes, but the apical margin turns outward as in *P. lowii.* As with the lateral petals the labellum of *Paphiopedilum niveum* seems to retain the morphology of a relatively early developmental stage, as it lacks the anterior lobing, and the apex is infolded. The development of labella of other brachypetalums is probably similar, but many clones of *P. godefroyae* and *P. concolor* have enlarged lateral margins where auricles would normally be located. *Paphiopedilum delenatii* exhibits no tendency for forming auricles. Anterior lobes are produced in most *Paphiopedilum* species as evidenced by their auricles. Even the "earless" *P. philippinense* forms slightly raised lateral margins, which differ from auricles only in their modest expression. The lateral lobes of *Paphiopedilum* never fuse during development unlike those of *Phragmipedium.*

The possession of anterior lateral lobes in *Phragmipedium* and *Paphiopedilum* suggests a relationship not shared with the plicate-leaved genera. However, the anterior lateral lobes develop to produce very dissimilar labella at anthesis. The persistence of earlier stages in mature flowers of *Paphiopedilum niveum* suggests that neoteny may have played a role in *Paphiopedilum* evolution. If this is true, floral features from advanced stages, which would have suggested relationships with other *Paphiopedilum* species, have become eliminated.

The homologies of the fertile stamens and staminode are apparent in buds of *Phragmipedium longifolium.* in the earliest stage observed, the three stamens appear similar in size and shape, but the central one lacks developing anther sacs. At a later stage, a constriction develops on the filament of the fertile stamens but not in the staminode. In the mature bud just prior to anthesis the staminode is much enlarged with a hispid pubescence. The lateral fertile stamens remain relatively small, and the previously constricted portion of the filament apparently serves as a hinge. Curiously, the mature staminode of *P. longifolium* subsp. *gracile* appear identical in shape with an immature staminode of the larger subspecies, and both may lack the hispid pubescence.

CHAPTER IV: CLADISTIC ANALYSIS AND THE CLASSIFICATION OF THE SLIPPER ORCHIDS

For methods on which to adumbrate slipper orchid relationships the following works on cladistics and evolutionary polarity have been consulted: Whiffin and Bierner, 1972; Crisci and Stuessy, 1980; Stevens, 1980; and Wagner, 1980. Cladograms are here constructed by the Wagner Groundplan-divergence method. As Wagner (1980) indicates, this method involving manipulation of data by hand allows one to think out the relationships for himself and may require less time than complex computer techniques. Furthermore, Lavarack (1971) produced several alternative dendrograms for the orchid family by computer analysis but did not recommend any major changes in orchid classification. As with any cladogram, the Wagner tree is considered only as a tool, and I will show that one of the assumptions in its construction is probably not justified when applied to the plicate-leaved species. The Wagner Groundplan-divergence method attempts to describe pathways of genetic change although one actually measures phenotypic characters.

The Wagner method makes two basic assumptions. (1) All members have a common ancestry. The unique slipper orchid flower justifies this assumption. (2) No hybridization occurred during evolution of the species. This assumption seems difficult to justify owing to the ease that species of *Paphiopedilum* may be hybridized. However, groups of species used as Operational Taxonomic Units (OTUs) are taxonomically definable, and the chances of "messy data" derived from past hybridizations are minimized.

The Wagner method involves three steps: (1) systematic analysis involving circumscription of OTUs, (2) determination of individual character trends, and (3) phylogenetic synthesis based upon divergences. Each procedure is described below.

SYSTEMATIC ANALYSIS

The adoption of OTUs is based on systematic treatments of Pfitzer (1903), Brieger (1971), and on data presented in chapters 2 and 3. It was shown that color patterns, shape, and size are often extremely variable within species, and that designation of species groups (subgenera and sections) on the basis of these criteria is not supported. However, since the pale colors of *Paphiopedilum* subgenus *Brachypetalum* are linked with other features which are interpreted as neotenic, they help define the group. The names ultimately to be adopted for the OTUs are not initially given taxonomic status and are referred to as "groups," which may include any taxon below genus to the level of species.

Criticism of traditional generic concepts. The conduplicate-leaved genera are natural as evidenced by morphological data and breeding relationships. *Phragmipedium* has the following unique character states: (1) valvate sepal vernation, (2) absence of sinuous epidermal cells in the perianth, (3) fused lateral lobes in the labellum, and (4) synsepals larger than the dorsal sepals. All species except the *Phragmipedium caudatum* complex have one or more bracts on the peduncle supporting the inflorescence, and all except *P. schlimii* have basal hollows in the lip. *Paphiopedilum* has the following unique character states: (1) imbricate sepal vernation, and (2) absence of vessels in the roots. It is otherwise distinguished from *Phragmipedium* by its parietal placentation in midovary sections, lack of peduncle bracts, non-fused lateral lobes, lack of basal hollows in the lip, and complex color patterns of the flowers.

The plicate-leaved genera are not as distinct. If *Cypripedium irapeanum* and *C. californicum* were removed, *Selenipedium* would have the following unique character states: (1) branched aerial stems below the inflorescence, (2) peripheral vascular bundles in the aerial stem, (3) root with uniseriate velamen, (4) plicate leaves with drip tips, (5) lip often with a pair of darkened patches, (6) a suberized endodermis in the aerial stem, (7) plant height greater than 1 meter, and (8) seeds with sclerotic testas. Of these features *Cypripedium irapeanum* has numbers 3, 4, 5, 6, and 7. *Cypripedium californicum* has numbers 2, 5, and often 7. The northern cypripediums are temperate and lack several anatomical features (at least at anthesis) which are universal in other slipper orchids. Unlike *Selenipedium* the ovaries are unilocular and the seeds lack sclerotic testas.

Circumscription of OTUs. The circumscription of OTUs will be guided by the following principles: (1) Monotypic OTUs should be avoided when based on singular features of shape, size and color patterns of flowers, which are considered trivial above the species level. (2) The units should reflect the similarities, not the differences among species. The infrageneric units will be based on distribution of unique character states, which may include vegetative, reproductive, or ecological features when known.

Selenipedium with six similar South American species is considered as one natural unit, but *Cypripedium irapeanum*, *C. californicum*, *C. arietinum*, *C. guttatum*, and *C. acaule* with questionable phenetic relationships are considered as separate OTUs. *Cypripedium candidum*, *C. montanum*, the *C. calceolus* complex, *C. reginae*, and the *C. macranthum* complex are similar in lip and staminode morphology and are interpreted as a single group (cypripedium group). Because the Asiatic plicate-leaved species and developmental data for *Cypripedium* have been unavailable, an in-depth critique of the relationships within *Cypripedium* cannot be undertaken, but the sample size is sufficient for comparison with the conduplicate-leaved genera.

Circumscription of OTUs within *Phragmipedium* is relatively simple compared with *Cypripedium* and *Paphiopedilum*. The emphasis on singular features, (e.g., staminode shape and presence of horns) in classifications by Pfitzer (1903), Brieger (1971), and Garay (1979) is not justified (*see* chapter 2). Similar emphasis on the slightly broadened petals, as in *P. sargentianum* and *P. lindleyanum*, does not justify sectional recognition.

Phragmipedium schlimii is unique in several features: (1) the petals are oval to orbicular, (2) the lip has light windows and lacks the hollow regions near the base, (3) the flower is pleasantly fragrant, and (4) the leaves have sculptured epidermal cells. The unique color patterns (white and pink) also distinguish this species. *Phragmipedium besseae* is similar in shape and size but is a brick or coral red. Both species are here placed in the micropetalum group.

The *Phragmipedium caudatum* alliance contains three distinct species as evidenced by lack of known intermediates (four species if one considers *P. wallisii* as separate from *P. lindenii*). The group is unique in having (1) extremely long petals, (2) simultaneous flowering habit, (3) unbranched inflorescences, and (4) very large adaxial epidermal cells in the leaves. These features are similar to those of *Paphiopedilum*, but most character states are consistent with *Phragmipedium*, not with *Paphiopedilum*. This complex is here termed the phragmipedium group because it contains the type species of the genus.

There is little to justify classification of the remaining species into separate groups, and all are here placed in the lorifolia group. This group has basically green flowers often suffused with red, the petals are somewhat elongated, and the petal tips often have a urinous aroma. It is distinguished by having character states opposite those mentioned above for the other two groups. *Phragmipedium* does not exhibit the diversity found in *Cypripedium* and *Paphiopedilum*.

In order to determine the natural species groups of *Paphiopedilum* worthy of taxonomic recognition, the works of Pfitzer (1903) and Brieger (1971) serve as a framework.

Pfitzer recognized *P.* subgenus *Brachypetalum*, which has three unique character states: (1) they have the broadest petals for their length in *Paphiopedilum*, (2) the lip apex is inturned, and (3) the ground color is white or nearly so. Although the labella lack conspicuous auricles, *P. concolor* exhibits slightly raised lateral regions. The brachypetalum group comprising approximately five species is natural and does not require further subdivision although *P. micranthum* is quite unique.

Pfitzer recognized a second subgenus (*P.* subgenus *Anotopedilum*), which is here called the coryopedilum group for nomenclatural reasons to be explained later. Its unique features include: (1) the staminode is deeply convex, (2) the staminode is laterally pubescent, (3) the ratio of dorsal sepal to synsepal area is smallest in *Paphiopedilum* (not including *P. delenatii* of the brachypetalum group), and (4) the petals are the narrowest in the genus for their length (except for *P. randsii*). Pfitzer recognized three sections in subgenus *Anotopedilum* based on singular peculiarities of staminode shape and on color distribution in the dorsal sepals. The resemblances outweigh the differences, and taxonomic recognition of subgroups within the coryopedilum group is not supported.

A third natural species group is *P.* section *Pardalopetalum* when united with *P.* section *Mastigopetalum.* This group (the pardalopetalum group) consisting of four species has (1) U-shaped petal bases, (2) a maximum petal width to petal length ratio between 0.1 and 0.2, (3) a lip with basal linear light windows, (4) a staminode with an apparent filament apex, and (5) an acute staminodial umbo. Although the two pairs of species relegated to different sections of the Pfitzer system appear strikingly different, the above unique features strongly support recognition as a single group.

A fourth group which Pfitzer called *P.* section *Cochlopetalum* contains one species and several subspecies (Wood, 1976). Although these may eventually be shown to deserve specific status, I am adopting Wood's taxonomy because it follows the rules of nomenclature. The most unique feature of the cochlopetalum group is the successional-flowered inflorescence developing 15 or more flowers. The cochlopetalum group also has rather short, spiraled petals.

Since Pfitzer relegated the remaining species not included in the above groups to several sections which are often monotypic, the remaining group circumscriptions will be based on Brieger (1971).

Brieger includes under *P.* subgenus *Paphiopedilum* the non-mottled-leaved species of the Southeast Asian mountains having one-flowered inflorescences. All species examined have a rounded umbo on the staminode although it may be cryptic. Brieger separates three species into *P.* section *stictopetalum* on the basis of having a pair of basal staminodial swellings, but the distinction is dubious. Brieger further relegates the non-mottled-leaved *P. fairieanum* to the next group (*P.* subgenus *Barbata*) on staminode shape, but the leaf color and presence of an umbo is consistent with the paphiopedilum group, not with the barbata group.

The last group under consideration is *P.* subgenus *Barbata.* Unique features of the barbata group include (1) sculptured epidermal cells in leaves, (2) lunate staminodes (lunate under a broad definition), and (3) production of warts on petals. Staminodial umbos are not apparent. The barbata group includes species with the largest dorsal sepal/synsepal area ratios in the genus. Although Pfitzer and Brieger distribute the approximately 30 species among three subgroups based on distribution and number of warts, cilia, and shape of petals, the species do not fall into three neatly-defined categories as some species exhibit mixed features. *Paphiopedilum ciliolare* may have either a slightly twisted or straight petal apex depending on the clone observed, and its taxonomic placement is subjective. Brieger places *P. acmodontum* with broad, twisted petal apices into *P.* section *Barbata* which, according to his key, is supposed to lack this feature. Although more than nine species complexes could be recognized, there is little gained by shoehorning the species into three or more sections.

Because evolution is a gradual process, it would be impossible to circumscribe natural groups of species were it not for extinction of "links." However, one might expect to find species or populations which are classified within particular species groups but which exhibit tendencies of a related group. *Phragmipedium longifolium* subsp. *gracile* seems to represent a step toward the micropetalum-type plant. *Paphiopedilum randsii*, although placed in the coryopedilum group, has shorter petals and slight expression of auricles similar to those of the cochlopetalum group. In the paphiopedilum group *P. fairieanum* has a lunate staminode similar to those of the barbata group with which it has been taxonomically placed (Brieger, 1971). *Paphiopedilum mastersianum* and the *P. violascens* complex (both in the barbata group) have similar color patterns and shape as *P. villosum* (paphiopedilum group). Despite these examples, the proposed species groups seem well defined and are adopted as Operational Taxonomic Units.

TREND ANALYSIS

In adumbrating evolutionary trends, the primitive (pleisiomorphic, pleisiomorphous) and derived (apomorphic, apomorphous) character states must be determined. As a starting point, I am following Whiffin and Bierner (1972) who suggest selection of the most primitive taxon. Because *Selenipedium* appears to be the most primitive taxon (e.g, Dressler and Dodson, 1960; Dressler, 1981), its associated character states will be considered primitive unless other evidence suggests that some of them are derived. Evolutionary polarity (see reviews by Crisci and Stuessy, 1980; and Stevens, 1980) is determined by appearance of teratological atavisms, possession of unique character states, and by data derived from developmental studies. Because there is only one very doubtful fossil slipper orchid (Schmid and Schmid, 1977) paleontology is not considered. The notion that a feature is primitive if it is most widespread in the study group is rejected unless it is correlated with other primitive features; otherwise the sclerotic testas and semi-baccate fruits of *Selenipedium* would be considered derived.

Out-group comparison (e.g. with *Vanilla*, *Epipactis*, Liliaceae, and Hypoxidaceae) suggests that *Selenipedium* has several features which are derived. The surface area of the synsepal in *Phragmipedium* resembles that of two of three equal-sized sepals in the Liliaceae, Hypoxidaceae, and most Orchidaceae. Furthermore, valvate sepal vernation as in *Phragmipedium* but not in *Selenipedium* is the rule in primitive orchids. *Cypripedium arietinum* has three primitive character states not present in *Selenipedium* nor in other slipper orchids: (1) separate lateral sepals, (2) a spurred lip, and (3) a staminode which so resembles the fertile stamens that pollen production would not be surprising.

On the basis of correlation of character states within the Cypripedioideae, the primitive perianth should be persistent. However, by out-group comparison this is consistent with *Epipactis* but conflicts with *Vanilla* which has deciduous perianths. It is doubtful that such a specialized feature was lost and secondarily regained in the Cypripedioideae or independently developed in *Vanilla*; thus it is interpreted as primitive despite lack of correlation of character states.

There are several apparent trend reversals in the slipper orchids. While most slipper orchid roots have vessels, *Paphiopedilum* roots lack them. I cannot offer an explanation for this observation made by Rosso, but the numerous derived character states of *Paphiopedilum* strongly suggest that such a reversal has occurred. The broadened petals of *Phragmipedium schlimii* and the brachypetalum group of *Paphiopedilum* apparently are trend reversals accounted for by neoteny. Although the flowers are more simple in construction than those of species to which they are related, the broadened petals are not similar to those of *Selenipedium.* At least one reason for interpreting each character state as primitive is coded in Table 4.1.

CONSTRUCTION OF WAGNER NETWORK

A taxon with all primitive character states is selected as the base of the Wagner Network. Since *Selenipedium* lacks five primitive character states found in other slipper orchids, a hypothesized ancestral taxon "Protoselenipedium I" is designated. The OTUs are evaluated according to their derived character states and given divergence formulas (Table 4.2). The linear distance of the OTUs from Protoselenipedium I is proportional to the total number of divergences (divergence levels). Reversal trends are included as independent steps when detected. The branching pattern is determined by tying together suites of derived character states under the assumption of parsimony.

Figure 4.1 shows a Wagner Network constructed as indicated above. The clade leading to *Cypripedium arietinum* originates from Protoselenipedium I because it has three primitive states not found in other slipper orchids, and the small epidermal cells and pericycle are similar to those of *Selenipedium*. Because the correlated primitive features of *C. arietinum* suggest the earliest divergence with the other slipper orchids, the necessary numerous parallel trends in vegetative characters with other *Cypripedium* species require a violation of parsimony. However, this apparent conflict will later be resolved.

There are several features which are clear concerning the conduplicate-leaved clade. (1) *Paphiopedilum* and *Phragmipedium* though distinct are closely related. (2) The coryopedilum group is most similar to *Phragmipedium* and is interpreted as most primitive in *Paphiopedilum.* (3) Within *Paphiopedilum* the barbata group is most derived and dissimilar to *Phragmipedium.* (4) The brachypetalums do not seem to fit anywhere into the cladogram. Their mottled leaves and broad spacing of vascular bundles seem derived, but the tendency for multiflowered inflorescences, especially in *P. concolor*, is primitive. The broadened petals resembling those found in early bud states in other groups suggest that neoteny has occurred, and that most floral features which could be used to assess relationships have been lost. The divergence level in the brachypetalum group is thus probably underestimated. (5) The lorifolia group is the most primtve group of *Phragmipedium* and lies almost directly in the implied evolutionary path between Protoselenipedium II and *Paphiopedilum.* The fit seems too comfortable to be explained by convergent evolution. Although the lorifolia group is distinguished from the hypothesized Protolorifolia group by three character states, the differences may be negligible. Fused lateral lobes may have existed in the ancestral groups but disappeared along the *Paphiopedilum* line when the anterior lateral lobes and apex became exerted. This single change would account for 2 of 3 character state differences. Furthermore, the loss of sinuous anticlinal walls in epidermal cells of flowers (the third character state) is not a great difference (see chapter 3). (6) Within *Phragmipedium* the micropetalum and phragmipedium groups are derived. Although the phragmipedium group has several character states in common with *Paphiopedilum*, to stem *Paphiopedilum* from the phragmipedium group would require several reversals, and the total number of required evolutionary steps would be greater. The assumption of parsimony requires that *Paphiopedilum* stem from the protolorifolia group, and the similarity of the phragmipedium and coryopedilum groups is interpreted as a convergence.

If the relationships of the conduplicate-leaved genera seem clear, those of the plicate-leaved genera are not. The clade suggesting a linear progression of evolution from Protoselenipedium II to *Cypripedium guttatum* seems unlikely. However, there are two aspects which are clear. (1) The conduplicate-leaved genera diverged from the plicate-leaved genera very early although *Cypripedium arietinum* must have diverged at an earlier time. (2) There is a geographic pattern that follows the non-*Cypripedium arietinum* clade; the most derived species (*C. guttatum*) occurs within the Arctic Circle while the primitive *Selenipedium* is tropical. Since *C. irapeanum* is Mexican, *C. californicum* hails from California and Oregon, and other cypripediums occur in more severe temperate climates, the clade seems to be related to increasing severity of climate. One can further ask the question "Are there similar geographic patterns observed in the same or between closely related taxa?" Two pairs of examples suggest that there are. *Cypripedium pubescens* may be 80 cm tall in the south, but its northern counterpart (*C. planipetalum*) apparently rarely exceeds 20 cm tall (Luer, 1975). Furthermore, the lateral petals are not deeply colored and lack the spiraling seen in more southerly populations suggesting a neotenic tendency in regions with short growing seasons. Intermediate plants grading toward *C. planipetalum* are found in northern Michigan, but the lateral petals are somewhat twisted. A similar situation is seen in *C. reginae* and *C. passerinum*. *Cypripedium passerinum* differs little from *C. reginae* aside from the pale flower color and dwarf size, both of which suggest neotenic tendencies. The range of *C. passerinum* nearly abuts on that of *C. reginae* but occurs to the north and west.

If reduction in the vegetative plant has occurred in several lines of *Cypripedium*, it should be possible to eliminate all those character states which are likely to be associated with the temperate climate (Table 4.3). Figure 4.2 shows the resulting cladogram. The sequence of relationships is the same as with Fig. 4.1, but the patristic distances are shortened. The non-vegetative derived states appear also to correlate with derived features associated with more severe climates. However, the position of *Cypripedium arietinum* now is consistent with the rule of parsimony providing a better justification for stemming this species from Protoselenipedium I.

Although the plicate-leaved clades suggest that *Cypripedium guttatum* is most derived and that *Selenipedium* is most primitive, there is some doubt that all adjacent OTUs actually represent close relationships. It seems probable that *C. irapeanum* stems directly from *Selenipedium*, and *C. californicum* may represent a neotenic derivative from a *Cypripedium irapeanum*-like ancestor, but the flowers of *C. guttatum* are far too unusual to suggest a relationship with *C. acaule* despite the common character states. Figure 4.3 de-

Table 4.1. Presumed primitive character states used for cladistic analysis.

Charac-ter Code	Primitive character state	Reasons for character choice: (A) occurs in Selenipedium; (B) outgroup analysis; (C) organs vestigial; (D) other	Tables in which characters are distributed
A	Plants tropical	A, B: Apostasioideae	2.1
B	Plant height may be more than 1 meter	A	2.1
C	Leaves 12 or more per sympodium	A, B: Apostasioideae	2.1
D	Leaf vernation convolute	A, B: Apostasioideae, *Curculigo*	2.1
E	Leaves cauline	A, B: Apostasioideae	2.1
F	Lower leaves with sheaths	A	2.1
G	Leaves and bracts not obligately distichous	A, B: Apostasioideae, *Epipactis*	2.1
H	Leaves plicate	A, B: Apostasioideae, *Epipactis*	2.1
I	Leaves with drip tips (attenuate)	A	2.1
J	Leaves without adaxial keel on midvein	A, B: Apostasioideae, *Epipactis*	2.1
K	Inflorescence multi-flowered	A, B: Apostasioideae, *Epipactis*	2.1
L	Inflorescence successional (applies to multi-flowered inflorescences only)	A, B: apparently Apostasioideae	2.1
M	Inflorescence may be a panicle of racemes	A, B: Apostasioideae	2.1
N	Leaves on stem holding the inflorescence not absent or reduced to bracts	A, B: Apostasioideae, *Epipactis*	2.1
O	Peduncle supporting the inflorescence not a scape	A, D: Scapes only associated with derived character states	2.1
P	Sepals valvate	B: *Epipactis*, most terrestrial Orchidaceae	2.2
Q	Sepals not with complex color patterns or three-dimensional shape	A, B: Apostasioideae, *Epipactis*	2.2
R	Area ratios of dorsal sepal to synsepal 0.9 or less (only applies to conduplicates)	B: Apostasioideae, *Epipactis* D: large dorsal sepals associated with derived states	2.2
S	Area ratios of dorsal sepal to synsepal 1.1 or less (plicates and *Paphiopedilum delenatii* excluded)	D: very large dorsal sepals associated with derived character states of *Paphiopedilum*	2.2
T	Lateral petals not warted	A, D: warts associated with derived states	2.2
U	Petal bases not transversely U-shaped at base	A, D: U-shaped only in *Paphiopedilum*	2.3
V	Lip apex not exerted	A, D: exerted only in *Paphiopedilum*	2.4
W	Auricles of lip absent ("horn" not considered	A	2.4
X	Anterior lateral lobes lacking	A	(See text in chapters 2 & 3)
Y	Light windows absent	A	2.4
Z	Lateral lobes of lip never fused	A, D: Fused only in *Phragmipedium*	2.4

Table 4.1. (Continued)

Character Code	Primitive character state	Reasons for character choice: (A) occurs in Selenipedium; (B) outgroup analysis; (C) organs vestigial; (D) other	Tables in which characters are distributed
A'	Velamen present	A	3.1
B'	Velamen uniseriate	A	3.1
C'	Root exodermis present	A	3.1
D'	Pericycle of highly-thickened cells	A	3.1
E'	Pericycle multiseriate	A	3.1
F'	Vessels present in root	A, D: lack of vessels only in *Paphiopedilum*	3.1
G'	Pith present in root	A	3.1
H'	Endodermis present in aerial stem	A	3.1
I'	Endodermis of aerial stem not suberized	A	3.1
J'	Aerial stem vascular bundles collateral	A	3.1
K'	Leaves with endoderm-like cells	A	3.1
L'	Leaf epidermal cell volume <.000,1 mm^3	A	3.2
M'	Leaf epidermal cell volume <.001 mm^3	D: huge associated with derived states	3.2
N'	Leaf epidermal cells lack sculpturing	A, D: sculpturing associated with derived states	3.2
O'	Leaf anticlinal walls of epidermal cells sinuous	A, D: associated with primitive states	3.2
P'	Leaves not mottled	A, D: mottled leaf associated only with most derived states	2.1
Q'	Ovaries trilocular in mid-section	A, B: Liliaceae in general	3.5
R'	At least some epidermal cell walls of perianth sinuous	A, B: *Epipactis helleborine*	3.5
S'	Staminode with a pair of recessed regions for anther sacs	C	(See chapter 2)
T'	Vascular bundles 1.5 per mm or more	A	(See Fig. 3.3 & 3.4)
U'	Perianth deciduous	A, D not associated with derived states	(See Chapter 1)
V'	Seeds with sclerotic testa	A, B: Liliaceae in general	(See Chapter 1)
W'	Aerial stem may be branched below the inflorescence	A, B: Apostasioideae?	(See Chapter 1)
X'	Lip lacking a pair of basal hollows	A, D: hollows only in *Phragmipedium*	2.4
Y'	Lip with darkened patches on orifice	A	(See text, Chapter 2)
Z'	Leaves not reduced to three or less	A, D: reduced associated with derived states in *Cypripedium*	---
A"	Staminode lacking longitudinal lamellae	A, D: lamellae associated with derived states	(See Chapter 2)
B"	Lip with a spur or appendage	B: Goodyerinae, *Epipactis*	(See Chapter 2)
C"	Staminode without a boss	D: boss associated with derived states	(See Chapter 2)
D"	Lateral sepals separate	B: subclass Liliidae and family Orchidaceae in general	(See Chapter 2)

Table 4.2. Divergence formulae and levels for 16 OTU's based on Table 4.1.

Group or OTU	Divergence formula	Divergence level
Selenipedium	P S' B" D"	4
Cyp. irapeanum	M P E' Q' S' V' W' B" D"	9
Cyp. californicum	A B/2 C I L M P A' C' D' E' H' K' L' Q' S' T' V' W' B" D"	20.5
Cyp. arietinum	A B C I K M A' C' D'/2 E' G' H' K' Q' T' V' W' Y'	17.5
Cyp. guttatum	A B C I K L M N O P Q A' C' D' E' G' H' K' L' Q' S' T' V' W' Y' Z' A" B" D"	29
Cyp. acaule	A B C I K L M N O P A' C' D' E' G' H' K' L' Q' S' T' V' W' Y' Z' B" D"	27
Most northern *Cypripedium*	A B C I K L M P Y/2 A' C' D' E' G' H' K' L' Q' S' T' V' W' Y' B" D"	24.5
Phragmipedium group	B C D E F G H I J L M N/2 X Z B' I' J' L' M' O' R' S' V' W' X' Y' B" D"	28.5
Lorifolia group	B C D E F G H I J X Z B' I' J' L' O' R' S' V' W' X' Y' B" D"	25
Micropetalum group	B C D E F G H I J X Z B' I' J' L' N' O' R' S' V' W' X' Y' B" D" Neotenic features: -(X/2 Z/2 X')	28
Coryopedilum group	B C D E F G H I J L M N O P Q R V X B' F' I' J' L' M' O' Q' S' T' V' W' Y' B" D"	34
Pardalopetalum group	B C D E F G H I J L M N O P Q R S T/2 U V W X Y B' F' I' J' L' M' O' Q' S' T' V' W' Y' B" C" D"	39.5
Cochlopetalum group	B C D E F G H I J L M N O P Q R S V W X B' F' I' J' L' M' O' P'/2 Q' S' T' V' W' Y' B" D" Reversal: -L	37.5
Paphiopedilum group	B C D E F G H I J K L M N O P Q R S V W X B' F' I' J' L' M' O' Q' S' T' V' W' Y' B" C" D"	38
Barbata group	B C D E F G H I J K L M N O P Q R S T V W X B' F' I' J' L' M' N' O' P' Q' S' T' V' W' Y' B" C" D" Reversal: -C"	42
Brachypetalum group	B C D E F G H I J K/2 L M N O P Q R S X/2 B' F' I' J' L' M' O' P' Q' S' T' V' W' Y' B" D" Reversals unknown	35

Facing page

Fig. 4.1 A cladogram based on the Groundplan-divergence method. Patristic distance (total number of character state changes) is represented by linear distance of taxa relative to hypothesized common ancestor "Protoselenipedium I", There is no particular significance to the angles of divergence selected. With one exception, the OTUs have been arranged to satisfy the rule of parsimony. Among the conduplicate-leaves taxa two trend reversals occur in *Phragmipedium* sect. *Micropetalum.* One trend reversal is hypothesized each for *Paphiopedilum* sect. *Cochlopetalum* and *P.* sect. *Barbata.* The relative positions of most OTUs seem fairly certain except for *Paphiopedilum* subgenus *Brachypetalum* and for *Cypripedium arietinum.* The former apparently neotenic group has undergone a number of unknown floral trend reversals obscuring relationships and divergence levels. To place *Cypripedium arietinum* in the main plicate-leaved clade would require several trend reversals, and its placement would be arbitrary. Since it has three character states which are more primitive than those of *Selenipedium,* plus two features of *Selenipedium,* it is interpreted as an ancient and independent line. This interpretation requires no trend reversals but violates the rule of parsimony. For a resolution of this problem see Fig. 4.2. The clade of the remaining plicate-leaved taxa connected by a dashed line is suspiciously linear and follows a latitudinal as well as morphological gradient.

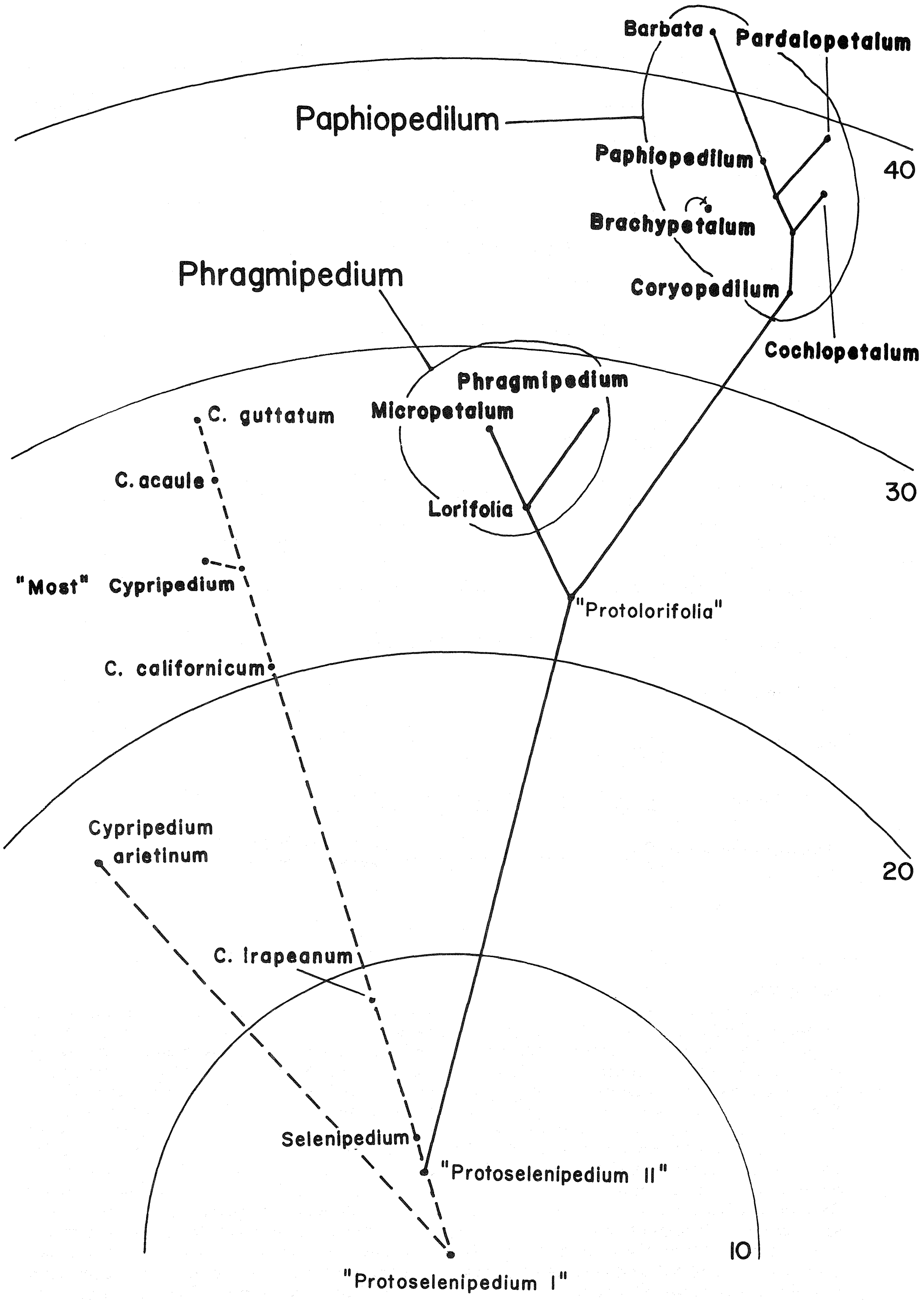
Barbata
Pardalopetalum
Paphiopedilum
Paphiopedilum
40
Brachypetalum
Phragmipedium
Coryopedilum
Cochlopetalum
Phragmipedium
C. guttatum
Micropetalum
C. acaule
30
Lorifolia
"Most" Cypripedium
"Protolorifolia"
C. californicum
Cypripedium arietinum
20
C. irapeanum
Selenipedium
"Protoselenipedium II"
10
"Protoselenipedium I"

Table 4.3. Divergence formulae and levels of the convolute-leaved OTU's with removal of features associated with the temperate habit. Character states eliminated are listed as follows: A B C I A' C' E' G' H' J' K' T' W' Z'. For character states see Table 4.1.

Group or OTU	Character state complex or formula	Divergence level
Selenipedium	P S' B" D"	4
Cyp. irapeanum	M P Q' S' V' B" D"	7
Cyp. californicum	L M P D' L' Q' S' V' B" D"	10
Cyp. arietinum	K M D'/2 Q' V' Y'	5.5
Cyp. guttatum	K L M N O P Q D' L' Q' S' V' Y' A" B" D"	16
Cyp. acaule	K L M N O P D' L' Q' S' V' Y' B" D"	14
Most northern *Cypripedium*	K L M P Y/2 D' L' Q' S' V' Y' B" D"	12.5

picts two extreme models (one monophyletic, the other polyphyletic) to explain the cladogram, but I suspect that an intermediate model will eventually be found to fit the plicate-leaved species. In chapter 6 both models will be discussed with reference to biogeography. It is probable that *Cypripedium* as presently circumscribed is polyphyletic.

OVERALL EVOLUTIONARY TRENDS

Several trends are apparent throughout the slipper orchids. (1) Reduction in plant size is evident, even within the conduplicate-leaved genera. (2) A trend toward the extreme growth habit of *Paphiopedilum* is notable when considering the relatively intermediate lorifolia group, which has cauline leaves (although reduced to bracts), small epidermal cells of the leaves, and close vascular bundles as in *Selenipedium.* In *Paphiopedilum* the peduncle lacks bracts below the inflorescence, the epidermal cells of the leaves are enlarged, and the vascular bundles are more distant. In *Phragmipedium* these trends toward a *Paphiopedilum*-type plant habit are also evident in the *Phragmipedium caudatum* complex. Mottled patterns and epidermal cell sculpturing in leaves occur only in the more derived groups. Apparently the mottled leaf has independently evolved in *Cypripedium margaritaceum* as it may have evolved at least three times in *Paphiopedilum*. Spacing of vascular bundles has narrowed in those species of *Phragmipedium* occurring in riverine habitats. (3) Increased floral specialization is evident in all lines. The dorsal sepal increases in size relative to the synsepal, warts or other embellishments develop in the more derived groups as do complex color patterns. Axile placentation has been lost at least three times in the slipper orchids as it has in other orchids.

THE ROLE OF NEOTENY IN SLIPPER ORCHID EVOLUTION

Neoteny appears to have played a major role in slipper orchid evolution. As with the *Cypripedium pubescens*-*C. planipetalum* and *C. reginae*-*C. passerinum* examples, similar ranges in variation are seen in *Phragmipedium* and *Paphiopedilum*, although unlike *Cypripedium* there is no apparent relationship with latitude. *Phragmipedium longifolium* var. *gracile* includes smaller plants and flowers than *P. longifolium* var. *longifolium.* The flow-

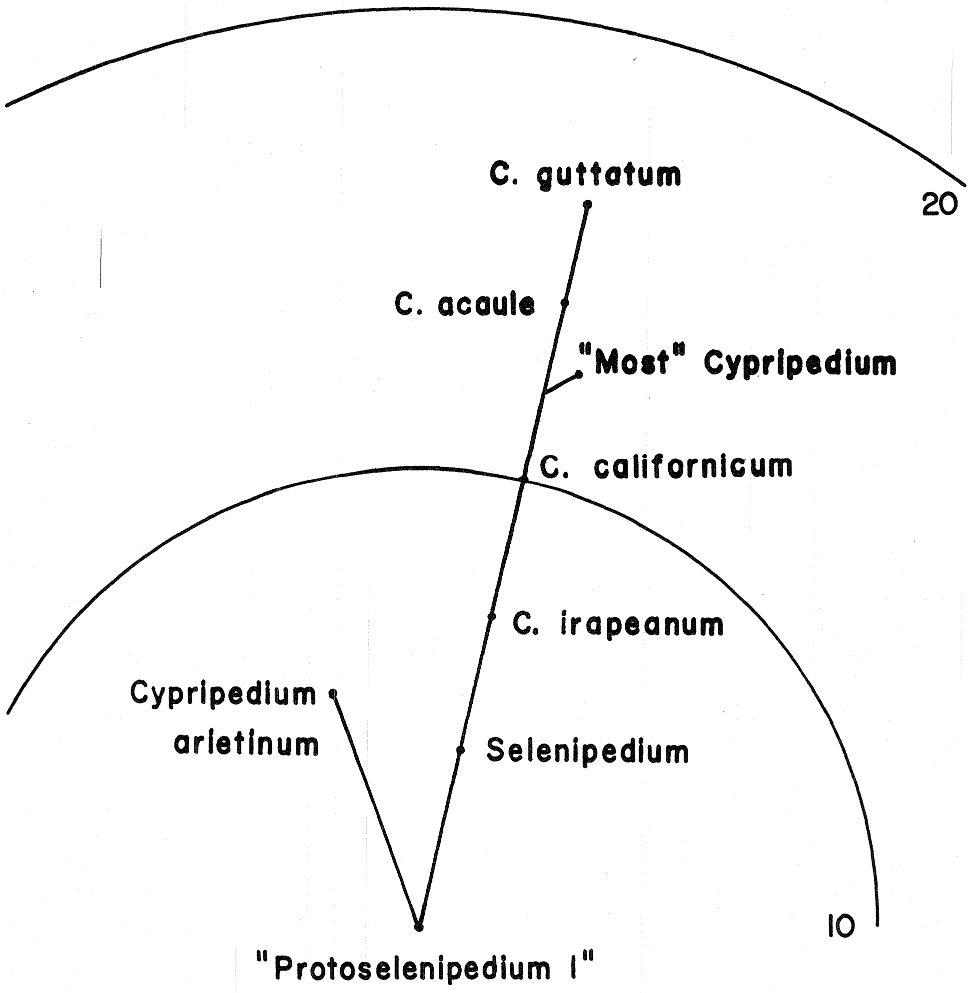

Fig. 4.2. A cladogram of the plicate-leaved OTUs with those character states eliminated which are correlated with latitude. Under this model, the divergence of *Cypripedium arietinum* is parsimonious. This model assumes convergent evolution in response to the temperate climate.

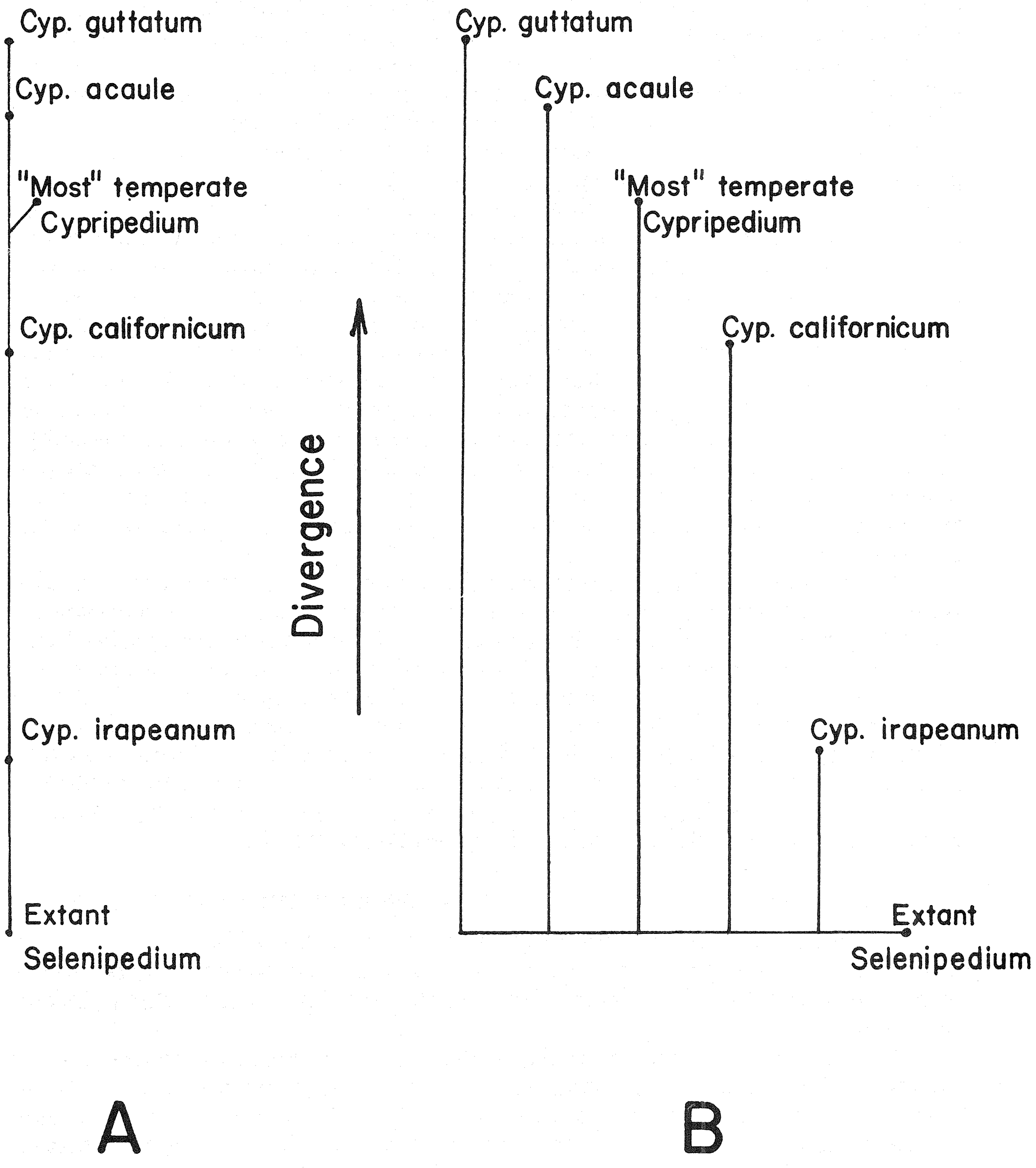

Fig. 4.3. Two models to explain the cladograms of the plicate-leaved species excluding *Cypripedium arietinum.* Vertical length represents relative patristic distance from *Selenipedium* based on Fig. 4.1. Model "A" is constructed according to the assumption of parsimony. Model "B" is based on two assumptions: (1) *Cypripedium* is polyphyletic, and (2), *Selenipedium* has remained unchanged.

ers are paler, have proportionally broader petals than the typical variety, and the staminode appears similar to that from a young bud stage in the larger variety. Since established plants may be destroyed relatively early in life from frequent flash flooding, neoteny might be explained as a response to r-selection in the unstable habitats of river beds. *Phragmipedium schlimii* seems to represent an extreme of neotenic tendencies in its flower while it is vegetatively specialized in its rugose epidermal cells. The *Paphiopedilum philippinense* and *P. glanduliferum* complexes exhibit similar kinds of size variation like *Phragmipedium longifolium.* In the former complex, the large-growing clones have very long, pendulous petals with many twists while in the miniature clones, the smaller flowers have nearly horizontally arranged petals with none or few twists, and the flower colors are paler. In the *P. glanduliferum* complex (including *P. praestans*) the larger flowers of the larger growing clones are strongly colored and have long, much-twisted petals which are pendulous. In the smaller growing clones (apparently including plants which are being called *P. wilhelminiae* and *P. gardneri* in horticulture) the green ground color is lacking, the petals are held horizontally and have few twists. The brachypetalum group appears to represent extreme neotenic tendencies. The plicate-leaved species are probably neotenic in their precocity of flowering and reduced plant size with climate severity. Although *Cypripedium fasciculatum* (not studied) occurs south of vegetatively more primitive taxa, other factors may eventually suggest selection pressures to account for its reduced size.

If neoteny can help us understand much of the variation patterns observed in the Cypripedioideae, its opposite (which I shall call "overdevelopment") has also played a role in evolution of the subfamily. *Phragmipedium warscewiczianum* is very much overdeveloped in its (1) much enlarged flowers, (2) proportionally much elongated lateral petals, and (3) strongly developed color patterns in the lip and lateral petals. *Phragmipedium wallisii* exhibits intermediate tendencies in its smaller flowers with less complex staminode and shorter petals. The paler floral colors may be evidence for neoteny. *Paphiopedilum sanderianum* (not known to exist presently except as herbarium specimens) exhibits similar elongated lateral petals.

IMPLICATIONS OF THE CLADOGRAM TO SLIPPER ORCHID CLASSIFICATION

Since the circumscription and relationships of the OTUs are now better understood, it is appropriate to suggest a classification which reflects the inferred phylogenetic relationships. For nomenclatural problems Stafleu (1978) has been consulted.

The generic distinction of *Paphiopedilum* and *Phragmipedium* is supported on structural and geographic grounds as well as on breeding relationships, and both are distinct from the plicate-leaved genera. One could argue for recognition of two tribes based on vegetative habit, but the recognition of a single tribe with corresponding subtribe for each of the four genera as recommended by Brieger (1971) is redundant. Tribal recognition is not recommended because the lorifolia group is vegetatively intermediate between *Selenipedium* and *Paphiopedilum.*

Among the plicate-leaved taxa it is clear that *Selenipedium* and *Cypripedium* are not distinct, but until the Asiatic species can be studied it is not wise to propose realignment of genera. However, because the evidence suggests that *Cypripedium arietinum* is not closely related to any extant group, it should be given generic status. The generic name of *Criosanthes* has already been proposed (Rafinesque, 1818), and the combination of *Criosanthes arietina* (R. Br.) House (1905) has been made.

For the three groups of *Phragmipedium* I recommend sectional status. Since *Cypripedium caudatum* Lindl. is the type species of *Phragmipedium*, the sectional name of *Phragmipedium* section *Phragmipedium* for the *P. caudatum* complex is automatic. The sectional name of *Phragmipedium* section *Micropetalum* has been given for *Phragmipedium schlimii.* The remaining species are here placed in *Phragmipedium* section *Lorifolia.*

Within *Paphiopedilum* I recommend two subgenera to distinguish the brachypetalums from the other groups since relationships are unclear. *Paphiopedilum* subgenus *Brachypetalum* does not require further sectional recognition. The remaining groups should be included in *Paphiopedilum* subgenus *Paphiopedilum* since the developmental evidence does not support further subgeneric subdivision on the basis of presence of enlarged auricles. This subgenus should include five sections. Since the green-leaved Himalayan species include the type for *Paphiopedilum (P. insigne)*, the group is designated *P.* section *Paphiopedilum.* Because the taxonomic levels of infrageneric groups published before Kraenzlin (1897) and Pfitzer (1903) were not designated, the names do not have priority, and the choice of the remaining four sectional names is narrowed. It is unfortunate that the designation of *P.* subgenus *Anotopedilum* Pfitzer cannot be transferred to sectional status, but Article 60.1 of the Leningrad Code (Stafleu, 1978) specifically states that "In no case does a name or an epithet have priority outside its own rank." Since Pfitzer (1903) published three sections under *P.* subgenus *Anotopedilum* in the same work (none of them named section *Anotopedilum*), any of the designations can be chosen. I have chosen the name *P.* section *Coryopedilum* Pfitzer because it includes the first described species in the section (sensu Pfitzer) and the name meaning "helmet shoe" is appropriately descriptive. Following is a taxonomic treatment of genera and infrageneric taxa of *Paphiopedilum* and *Phragmipedium.* Appendix 9 lists the species which should be included in each infrageneric taxon.

Cypripedium L., Species Plantarum 2: 951, 1753.
  Type: *Cypripedium calceolus* L. including *Saccodon* Raf.

Criosanthes Raf., Amer. Monthly Mag. & Crit. Rev. 268, 1818.
  Type: *Cypripedium arietinum* R. Br.

Selenipedium Rchb. f., in part, Xenia Orchidacea 1: 3, 1854.
  Type: *Selenipedium chica* Rchb. f.

Phragmipedium Rolfe, Orchid Rev. 4: 331, 1896 (nom. cons.)
  Type (cons.): *Cypripedium caudatum* Lindl.
  Syn.: *Phragmopedilum* Pfitz.
    Uropedium Lindl.
   section *Phragmipedium.*
    Syn: *Cypripedium* section *Caudata* Krzl., in part;
      Phragmopedilum Pfitz. section *Desmopedilum* Pfitz.
   section *Lorifolia* (Krzl.) Garay (s. amplo).
    Type: *Cypripedium longifolium* Rchb. f. & Warsz.
    Including: *Phragmopedilum* section *Ceratopedilum* Pfitz., *Phragmopedilum* section *Himantopedilum* Pfitz., and *Phragmopedilum* section *Platypetalum* Pfitz.

section *Micropetalum* (Hall.) Garay.
Type: *Selenipedium schlimii* Lind. & Rchb. f.
Syn.: *Phragmopedilum* section *Micropetalum* (Hall.) Pfitz.
Phragmipedium subgenus *Micropetalum* (Hall.) Brieg.

Paphiopedilum Pfitz., Morph. Stud. Orch. 11, 1886 (nom. cons.).
Type (cons.): *Cypripedium insigne* Wall. ex Lindl.
subgenus *Paphiopedilum*
section *Paphiopedilum*
Syn.: *Cypripedium* section *Insignis* Krzl., in part
Paphiopedilum subgenus *Paphiopedilum* (sensu Brieger).
Including: *P.* section *Neuropetalum* (Hall.) Pfitz., *P.* section *Stictopetalum* (Hall.) Pfitz., *P.* section *Thiopetalum* (Hall.) Pfitz., *P.* section *Cymatopedilum* (Hall.) Pfitz., and *P.* section *Ceratopetalum* (Hall.) Pfitz.
section *Barbata* (Krzl.) Atwood *exclusis speciebus*.
Type: *Cypripedium barbatum* Lindl.
Including: *P.* section *Spathopetalum* Pfitz., *P.* section *Blepharopetalum* Pfitz., *P.* subgenus *Barbata* (Krzl.) Brieger *exclusis speciebus*, and *P.* section *Phacopetalum* Pfitz.
section *Cochlopetalum* (Hall.) Pfitz. (s. amplo).
Type: *Cypripedium victoria-regina* Sander.
section *Coryopedilum* Pfitz. (s. amplo).
Type: *Cypripedium glanduliferum* Blume.
Syn.: *P.* subgenus *Anotopedilum* Pfitz.
section *Pardalopetalum* (Hall.) Pfitz. (s. amplo).
Type: *Cypripedium lowii* Lindl.
Including: *P.* section *Mystropetalum* Pfitz.
subgenus *Brachypetalum* (Hall.) Pfitz.
Type: *P. concolor* (Batem.) Pfitz.

KEY TO GENERA AND TO INFRAGENERIC TAXA OF THE CONDUPLICATE-LEAVED GENERA

1. Leaves thin, plicate, cauline, although often appearing basal, often spiraled on the stem at least near the stem apex, the lowermost with sheaths; perianth persistent; sepals with perforate vernation; lip with only one pair of lateral lobes at the base (at least in the New World representatives) 2
  2. Plants tropical, usually above 1 m tall, with more than 12 leaves; inflorescence multiflowered and successional; ovary trilocular in midovary section; seeds with sclerotic testas . . . . *Selenipedium*
  2a. Plants temperate except *Cypripedium irapeanum*; ovary unilocular in midsection; seeds lacking sclerotic testas 3
    3. Flowers with separate lateral sepals; lip spurred . . . . *Criosanthes*
    3a. Flowers with synsepals; lip not spurred . . . . *Cypripedium*

1a. Leaves conduplicate, basal, always distichous as are the floral bracts, sheaths absent, except for slight development in peduncle bracts of *Phragmipedium*; perianth deciduous; sepals with valvate or imbricate vernation; lip usually developing an extra pair of anterior lobes in bud 4

4. Ovaries always 3-locular in midovary section; sepal vernation valvate, synsepal much larger than the dorsal sepal; lobes of lip fused in the bud, a pair of hollow regions occurring at the base of the lips except in *Phragmipedium schlimii*; peduncle with one or more bracts; vascular bundles of leaves usually 1.5 per mm in cross-section .... *Phragmipedium* (Key 1 for sections)
4a. Ovaries always unilocular in midovary sections; sepal vernation imbricate, sepals subequal in size or the dorsal much enlarged; lateral lobes of the lip not fused, no hollow regions occurring at the lip base; peduncle rarely with one bract near the base of the scape; vascular bundles of leaves usually fewer than 1.5 mm per mm in cross-section .... *Paphiopedilum* (Key 2 for sections)

Key 1: *Phragmipedium*

1. Lateral petals oval to orbicular .... section *Micropetalum*
1a. Lateral petals much longer in proportion to width 2
    2. Petals less than 15 cm long; inflorescences often branched (rarely in *P. longifolium*), successional-flowered .... section *Lorifolia*
    2a. Petals at least 20 cm long; inflorescences not branched; simultaneous-flowered .... section *Phragmipedium*

Key 2: *Paphiopedilum*

1. Flower color white to light yellow or pink, usually lateral petals 1/2 or more times as wide as long .... subgenus *Brachypetalum*
1a. Flowers otherwise .... (subgenus *Paphiopedilum*) 2
    2. Inflorescence 2 or more flowered 3
        3. Inflorescence successional-flowered .... section *Cochlopetalum*
        3a. Inflorescence usually with all flowers open at once 4
            4. Labellum lacking conspicuous auricles, lacking light windows; staminode lacking an umbo but very concave and with a conspicuous lateral pubescence .... section *Coryopedilum*
            4a. Labellum with conspicuous lateral auricles (ears), and with light windows or translucent lines; staminode with an acute umbo .... section *Pardalopetalum*
    2a. Inflorescence usually single-flowered; auricles always present 5
        5. Leaves not mottled, epidermal cells of leaves not sculptured; staminode not lunate (except in *P. fairieanum*), blunt umbo usually apparent .... section *Paphiopedilum*
        5a. Leaves mottled, with scultured epidermal cells; staminode lunate, umbo lacking .... section *Barbata*

CHAPTER V: KARYOLOGY

Although the chromosomes of most orchids are small and difficult to karyotype, those of the Cypripedioideae are large. For this reason the Cypripedioideae has received much attention by cytologists since the nineteenth century. For literature reviews see Duncan (1959) and Tanaka and Kamemoto (1974). In this chapter I will show that the karyological evidence is consistent with the classification proposed in chapter 4.

PLICATE-LEAVED GENERA

Chromosome numbers are known for 16 species of *Cypripedium*. The earlier accounts by Pace (1907) and Hoffman (1929) seemed to indicate that *Cypripedium* has 22 chromosomes in somatic tissues, but Humphrey (1932) found 20 in *Cypripedium acaule*, *C. pubescens*, and *C. candidum*. With two known exceptions, most species have 20 chromosomes. There is a report of 26 chromosomes in *C. speciosum* (Mulay and Panikkar, 1953), but this should be confirmed. Belaeva and Siplivinsky (1976) have reported 30 chromosomes for *C. guttatum*, which is probably a triploid. The basal chromosome number of *Cypripedium* is apparently $2n = 20$.

Although more work needs to be done on chromosome morphology, the centromeres all appear to be interstitial and no telecentrics are known to occur in *Cypripedium*. Arm ratios have been determined for *C. cordigerum* but appear to be variable depending on the clone investigated (Mehra and Bawa, 1970; Vij and Gupta, 1976). *Cypripedium* chromosomes are usually reported as "large" but few actual measurements have been taken. Humphrey (1932) reported that chromosomes of *Cypripedium acaule*, *C. candidum*, and *C. pubescens* are 7 to 10 μm long, thus the estimated total length of 20 chromosomes is between 140 and 200 μm. Vij and Mehra (1974) indicated that chromosomes sizes in *C. cordigerum* and *C. himalaicum* range respectively from 9.2 to 16.4 μm and 8 to 15.8 μm. The estimated total lengths for 20 chromosomes lie between 184 and 328 μm for *C. cordigerum* and 160 and 316 μm for *C. himalaicum*. From the data provided by Vij and Gupta (1976) the total length of the chromosomes of *C. cordigerum* is between 200 and 262 μm, which agrees with the previous report. Nothing is known of the karyology of *C. irapeanum*, *C. californicum*, or *Selenipedium*, but Love and Simon (1968) report $2n = 20$ for *Criosanthes arietina (Cypripedium arietinum)*.

**PHRAGMIPEDIUM*

Few chromsome numbers are known for *Phragmipedium*. Hoffmann (1930) reported $2n = 32$ for *P. caudatum* and $2n = 24$ for *P.* × *sedenii*. Brown (in Duncan, 1959) reported $2n = 20$ in *P. longifolium*, and Karasawa and Tanaka (1976) have shown that *P. boissieranum* has $2n = 18$, the lowest report in the Cypripedioideae.

I have investigated the chromosomes of five species of *Phragmipedium* (Table 5.1). Root tips were pretreated in 0.002 M 8-hydroxyquinoline at 0° C for 10 hours, fixed in acetic alcohol (1:3), squashed in propiono-carmine, and observed with a Wild M20 binocular microscope. Occasionally root tips were hydrolized in 10% HC1 for 5 minutes before squashing to spread the chromosomes for viewing. Camera lucida drawings were made from the karyological preparations. Chromosome arm lengths were determined from the camera lucida drawings and summed to determine the total length of both genomes. Mean arm ratio (the average of the ratios of the long arm to short arm per diploid karyotype) was calculated in various karyotypes excluding telocentric chromosomes, which may have originated by fission of metacentrics. Figure 5.1 shows several idiograms prepared from camera lucida drawings.

---

* Since this dissertation was concluded, a work entitled "Karyomorphological Studies in *Phragmipedium*, Orchidaceae" by K. Karasawa was sent to me by the author (Bulletin of the Hiroshima Botanical Garden, 3: 1-49). The reader is encouraged to read this account as we differ in interpretation of centromere position of chromosomes 9 and 10, for instance, in *Phragmipedium hartwegii* (p. 23).

Table 5.1. Karyotypic data of five *Phragmipedium* species. For geographic origins see Appendix 10.

Species	Clone number	2n	n	Number of cells	Number of metacentrics	Number of telocentrics	Mean arm ratio excluding telocentrics	Total chromosome length
P. caricinum	7620	20	-	2	18	2	1.76	88.6
	77189	22	-	4	-	-	-	-
	77900	20	-	3	18	2	-	100.1
	7619	20	-	2	20	0	2.025	103.9
P. longifolium								
typical	77173-3	20	-	5	18	2	1.78	80.7
typical	N-1	20	-	4	18	2	1.74	94.3
intermediate	781-1	20	-	3	18	2	1.81	105.1
gracile	77177-4	20	-	24	18	2	-	-
gracile	77177-7	20	-	4	18	2	-	-
hartwegii	7623-3	20	-	2	18	2	1.73	86.6
P. pearcei	7622	22	-	3	18	4	-	108.2
P. schlimii	747	30	-	11	-	-	-	68.54-85.34
P. warscewiczianum	782	28	-	2	-	-	-	-
"	782		14	4	-	-	-	-

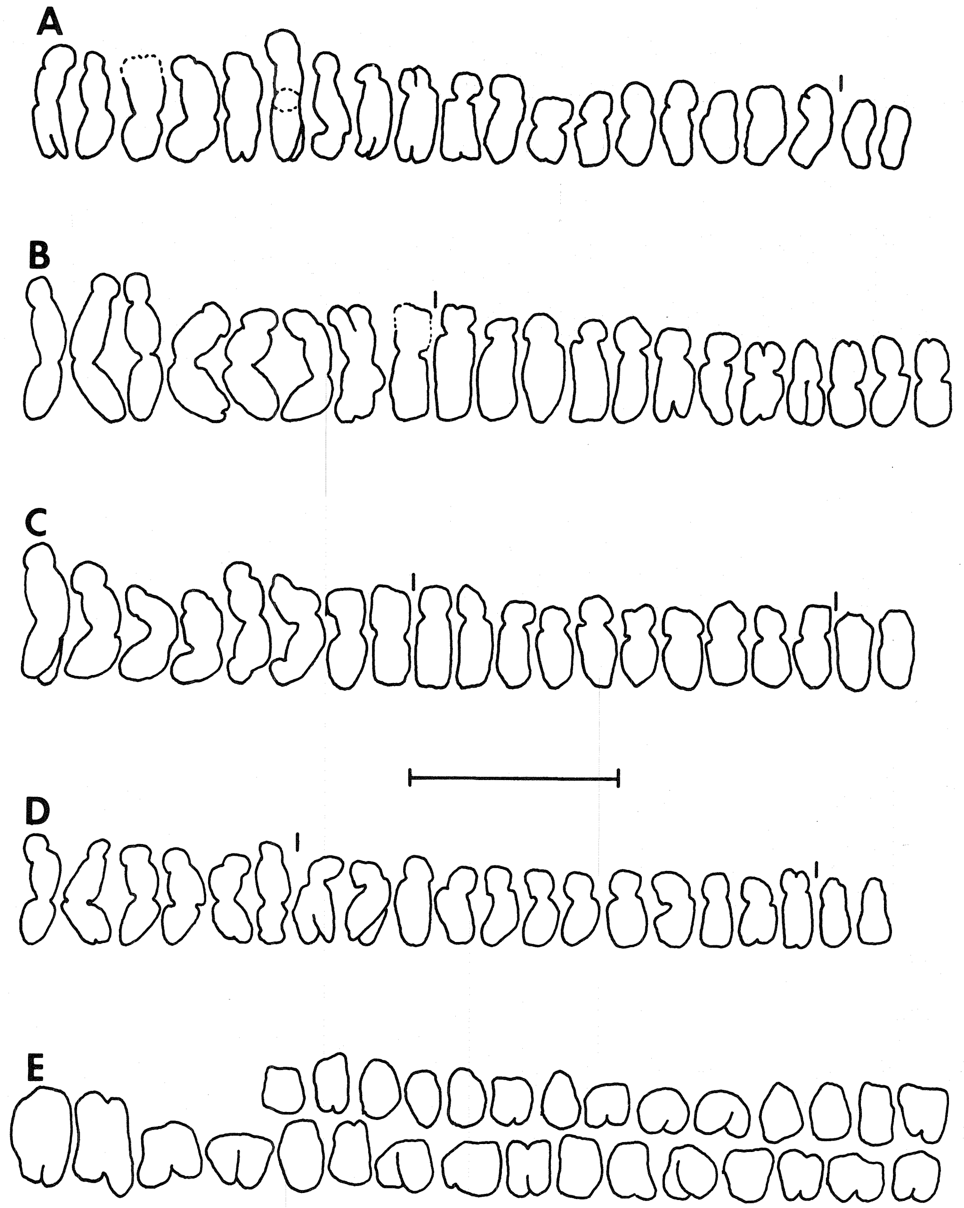

Fig. 5.1. Idiograms of three species of *Phragmipedium*. Tick marks indicate discontinuities in chromosome morphology. The scale is about 10 micrometers. A. *Phragmipedium caricinum* clone 77900 (2*n* = 20). All chromosomes have interstitial centromeres except for the last pair which is telocentric. The long chromosome (number 6) was observed in all cells and has a darkly staining central region. This and the adjacent dumbbell-shaped chromosome (number 7) had no homologues and may have translocations. B. *Phragmipedium caricinum* clone 7619 (2*n* = 20) with 8 large metacentrics, and 12 chromosomes with one arm of nearly constant length. All chromosomes have interstitial centromeres. C. *Phragmipedium longifolium* clone 77173-3 (2*n* = 20), a large embankment plant from El Valle, Panama, with 8 large megacentrics, 10 smaller metacentric to submetacentric chromosomes with one arm of nearly constant length and a pair of telocentrics. One clone of *P. caricinum* was indistinguishable from this. D. *Phragmipedium longifolium* subsp. *gracile* clone 77177-7, a small-growing river bed plant with an idiogram differing from the previous only in having two fewer large metacentrics. E. *Phragmipedium schlimii* clone 747 (2*n* = 30). Centromere position was largely indeterminable.

The four clones of *Pragmipedium caricinum* examined exhibit karyological diversity. One has $2n = 22$; the remaining three have $2n = 20$ chromosomes. Of the latter three clones, two have a pair of telocentrics and one has none. The karyotype of one clone appears essentially indistinguishable from that of *P. longifolium.* The total length of both genomes and arm ratio is 88.6 μm and 1.76 in clone 7620, and 103.9 μm and 2.0 in clone 7619, but these differences may be as much accounted for by preparation technique as by actual genetic differences. *Phragmipedium pearcei*, which is morphologically similar to *P. caricinum*, was found to have $2n = 22$ chromosomes, similar to one clone of the latter species.

All the examined clones of *P. longifolium* were karyologically similar despite diverse clone selection from Ecuador and Panama. All have 20 chromosomes; 18 with interstitial and 2 with terminal centromeres. Only one difference was noted in a single specimen of entity *gracile*, which has one less pair of large metacentrics. Length of both genomes and mean arm ratio were similar among the six clones examined.

The chromosome number of *P. schlimii* was found to be $2n = 30$. Although the morphologies differ from those of the other species examined, centromere position was not determinable. The orientation of the arms was also difficult to assess since many chromosomes had a square appearance. Since each chromosome could have two interpretations of length, both minimum and maximum lengths were determined for each chromosome, from which the minimum and maximum lengths of both genomes were determined. The length of both genomes was found to lie between 68.5 and 85.4 μm. Arm ratio could not be determined.

In somatic tissues *P. warscewiczianum* has $2n = 28$ chromosomes, which were not sufficiently contracted to estimate genome length or arm ratios. They appeared smaller than those of *P. longifolium*, *P. caricinum* and *P. pearcei.*

Phragmipedium longifolium is karyologically uniform, unlike *P. caricinum.* The single clone of *P. pearcei* examined is karyologically similar to one clone of *P. caricinum*, and extensive field studies may eventually show these latter species to intergrade. I cannot suggest an explanation for the differences in chromosome number of *P. schlimii*, but the total length of both genomes argues against polyploidy. The smaller chromosomes of *P. warscewiczianum* also suggest a type of chromosomal repatterning not involving polyploidy. The very different chromosome numbers of *P. schlimii* and *P. warscewiczianum* support sectional distinction, and the similar karyology of the *P. caricinum* complex, *P. pearcei* and *P. longifolium* supports inclusion under one section. The basal chromosome number of *Phragmipedium* is probably 20.

PAPHIOPEDILUM

A review of the karyology of *Paphiopedilum* to 1929 is given by Hoffmann (1930). The cytology of the earlier workers has been found to be nonrepeatable, and many published chromosome numbers are probably incorrect. Francini (1934) produced the first in-depth paper on the chromosomes of *P. villosum*, *P. barbatum*, and the primary hybrid *P.* × *harrisianum* and recognized the difference between metacentrics and telocentrics. Her observations have been repeated. Duncan (1945, 1947) and Duncan and MacLeod (1948a, 1948b, 1949a, 1949b, 1949c, 1950a, 1950b) surveyed many species of *Paphiopedilum.* Although several of their observations have not been repeated, they noted that one-armed chromosomes were characteristic of *Paphiopedilum* section *Cochlopetalum* and *P.* section *Barbata.* The most accurate and

Table 5.2. Diploid number, arm number, and morphology of *Paphiopedilum* chromosomes according to Karasawa (1979). Genome length and mean arm ratio of metacentrics were derived from data by Karasawa.

Taxon	2n	Arm number	Chromosomes with 2 arms	Telocentrics	Total chromosome length	Mean arm ratio of metacentrics
Brachypetalum group						
bellatullum	26	52	26	0	162.7	1.12
concolor I	26	52	26	0	167.2	1.25
concolor II	26	52	26	0	200.6	1.40
delenatii	26	52	26	0	159.5	1.28
godefroyae	26	52	26	0	251.1	1.22
'ang-thong'	26	52	26	0	190.0	1.22
'*leucochilum*'	26	52	26	0	164.2	1.12
niveum	26	52	26	0	166.9	1.21
Coryopedilum group						
bodegomii	26	52	26	0	212.7	1.29
glanduliferum	26	52	26	0	168.6	1.24
laevigatum	26	52	26	0	209.2	1.39
philippinense	26	52	26	0	186.6	1.40
praestans	26	52	26	0	194.6	1.19
randsii	26	52	26	0	172.4	1.33
roebbelenii	26	52	26	0	212.4	1.38
rothschildianum	26	52	26	0	201.6	1.21
stonei	26	52	26	0	170.8	1.16
Pardalopetalum group						
haynaldianum	26	52	26	0	198.5	1.42
lowii	26	52	26	0	169.0	1.44
parishii	26	52	26	0	251.2	1.59
Cochlopetalum group						
victoria-regina						
ssp. *liemianum*	32	50	18	14	149.1	--
ssp. *primulinum*	32	50	18	14	159.7	--
" f. *purpurascens*	32	48	16	16	189.1	--
ssp. *chamberlainianum*	34	50	16	18	152.1	--
ssp. *glaucophyllum*	36(37)	50	14	22	171.4	--
" var. *moquetianum*	34	50	16	18	146.2	--
ssp. indet.	33	49	16	17	164.3	--
ssp. indet.	35	50	15	20	166.2	--
ssp. indet.	36	50	14	22	186.0	--

Taxon	2n	Arm number	Chromosomes with 2 arms	Telocentrics	Total chromosome length	Mean arm ratio of metacentrics
Paphiopedilum group						
boxalii	26	52	26	0	167.9	1.17
charlesworthii	26	52	26	0	198.4	1.26
druryi	30	52	20	8	194.9	1.46
esquirolei	26	52	26	0	163.9	1.15
exul	26	52	26	0	170.6	1.17
fairieanum	26	52	26	0	180.9	1.42
hirsutissimum	26	52	26	0	177.7	1.69
insigne	26	52	26	0	201.8	1.19
spicerianum	30	52	20	8	205.7	1.21
villosum	26	52	26	0	177.0	1.23
Barbata group						
acmodontum	36	52	16	20	177.5	1.25
appletonianum	38	52	14	24	204.5	1.23
argus	38	52	14	24	282.8	1.49
barbatum	38	52	14	24	197.1	1.35
bougainvilleanum	40	52	12	28	282.0	1.91
bullenianum	40	52	12	28	231.8	1.23
callosum	32	52	20	12	168.6	1.21
celebesense	42	52	10	32	178.7	1.28
ciliolare	32	52	20	12	268.4	1.4
curtisii	36	52	16	20	231.6	1.29
dayanum	36	52	16	20	227.9	1.33
hennisianum	36	54	18	18	229.6	1.92
hookerae	28	56	28	0	209.7	1.53
javanicum	38	52	14	24	237.4	1.13
lawrenceanum	36	52	16	20	244.6	1.45
mastersianum	36	52	16	20	255.6	1.61
purpuratum	40	52	12	28	279.7	1.68
sukhakulii	40	52	12	28	180.3	1.15
superbiens	38	52	14	24	219.3	1.4
tonsum	32	52	20	12	200.9	1.27
venustum	40(41)	52	12	28	314.6	1.47
violascens	38	52	14	24	242.6	1.69
virens	40	52	12	28	219.4	1.53
wentworthianum	40	52	12	28	283.2	1.63

Table 5.3. Karyological report of nine species of *Paphiopedilum*. For presumed geographic origins, see Appendix 10.

Species	Clone number	Chromosome number	Arm number	Non-telocentrics	Telocentrics	Number of cells	Total chromosome length (μm)	Mean arm ratio
P. acmodontum	741-4	36	—	—	—	5	—	—
	741-5	36	—	—	—	8	—	—
	741-8	36	—	—	—	2	—	—
P. appletonianum	78102	38	—	—	—	6	—	—
	78101	38	52	14	24	1	196.1	1.16
	78101	38	52	14	24	1	200.5	1.21
P. argus	732-0	38	—	—	—	1	—	—
	732-2	38	52	14	24	9	269.8	1.42
	732-2	38	52	14	24	9	224.8	1.36
	732-2	38	52	14	24	9	321.8	1.42
P. hennisianum	731	36	54	18	18	3	210.1	1.76
P. sukhakulii	76293	40	—	—	—	6	—	—
P. tonsum	733	32	52	20	12	3	178.3	1.31
P. venustum	s.n.	40	—	—	—	3	—	—
P. victoria-regina ssp. *liemianum*	736	32	—	—	—	3	149.1	—
P. wardii	SEL 78-615	44	—	—	—	3	230.6	—

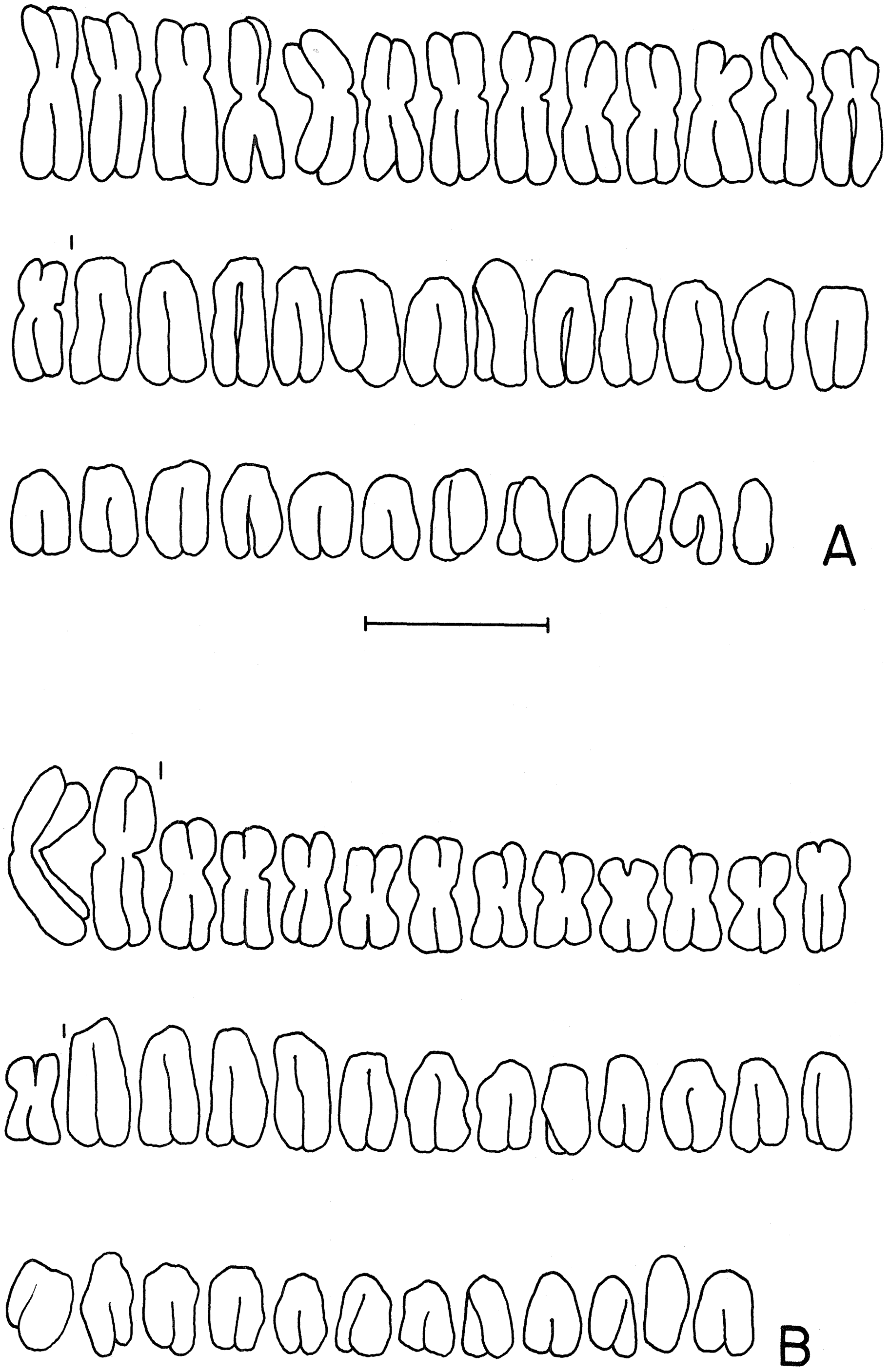

Fig. 5.2. Idiograms of two species of *Paphiopedilum* section *Barbata.* Tick marks indicate discontinuities in chromosome morphology. The scale is approximately 10 micrometers. A. *Paphiopedilum argus* clone 732-2 (2*n* = 38; arm number = 52). The size range of the metacentrics is continuous. B. *Paphiopedilum appletonianum* clone 78161 (2*n* = 38; arm number = 52). There is a discontinuity in the size of metacentrics unlike the karyotype of *P. argus.*

Table 5.4. Genome lengths and arm ratios in *Paphiopedilum* groups (based on data of Karasawa, 1979).

Group	Mean ($\bar{X}$) length of two genomes ± one standard deviation (um)	Range of the means of two genomes	Mean arm ratio ± one standard deviation
Brachypetalum (n=9)	181.74±33.57	159.5-251.1	1.23±.09
Coryopedilum (n=9)	192.1±18.2	168.6-212.7	1.28±.093
Pardalopetalum (n=3)	206.233±41.6	169.0-251.2	1.48±.093
Cochlopetalum (n=9)	162.3±14.0	146.2-189.1	--
Paphiopedilum (n=9)	184.2±16.0	163.9-205.7	1.28±.179
Barbata (excluding *P. fairieanum*) (n=25)	230.0±39.7	168.6-314.6	1.43±.220

Table 5.5. Data for deriving differences in mean arm lengths of telocentrics and metacentrics in *Paphiopedilum* sect. *Barbata*. The data are based on Karasawa (1979).

Species	Metacentric number	Mean metacentric arm length ($\overline{X}$)	Telocentric number	Mean telocentric arm length ($\overline{Y}$)	T' "T" test	Degrees of freedom $\frac{m+n}{2}$	α Significance	$\overline{Y}-\overline{X}$
P. acmodontum	16	3.18	20	3.79	2.005	34	$<.025$	.61
P. appletonianum	14	3.24	24	4.74	3.686	36	$<.0005$	1.5
P. argus	14	4.68	24	6.325	3.545	36	$<.001$	1.645
P. barbatum	14	3.49	24	4.14	1.798	36	$<.05$	.65
P. bougainvilleanum	12	4.55	28	6.175	3.579	38	$<.0005$	1.625
P. bullenianum	12	3.4	28	5.36	5.164	38	$<.000,01$	1.96
P. callosum	20	2.915	12	4.33	3.852	30	$<.0005$	1.415
P. celebesense	10	2.58	32	3.97	4.198	40	$<.01$	1.39
P. ciliolare	20	4.855	12	6.18	2.529	30	$<.01$	1.325
P. curtisii	16	3.79	20	5.51	4.317	34	$<.0001$	1.72
P. dayanum	16	4.12	20	4.81	1.896	34	$<.05$	.69
P. hennisianum	18	3.869	18	5.02	2.842	34	$<.005$	1.151
P. javanicum	14	3.89	24	5.36	3.362	36	$<.001$	1.47
P. lawrencianum	16	4.10	20	5.665	3.815	34	$<.0005$	1.565
P. mastersianum	16	4.3	20	5.9	3.560	34	$<.001$	1.6
P. purpuratum	12	5.1	28	5.62	1.073	38	$<.25$	.52
P. sukhakulii	12	3.25	28	3.66	1.326	38	$<.10$	.41
P. superbiens	14	3.37	24	5.204	5.073	36	$<.000,01$	1.834
P. tonsum	20	3.55	12	4.91	3.688	30	$<.0005$	1.36
P. venustum	12	5.92	28	6.36	.9765	38	$<.25$	.44
P. violascens	14	4.21	24	5.20	2.20	36	$<.025$	.99
P. virens	12	3.27	28	5.036	4.466	38	$<.000,05$	1.766
P. wentworthianum	12	4.96	28	5.86	1.837	38	$<.05$	.9

repeatable reports have been made by Mehlquist (1947), McQuade (1949), Kamemoto et al. (1963), and by more recent investigators. The most comprehensive investigation has been made by Karasawa (1979). Table 5.2 shows the distribution of chromosome numbers, numbers of metacentrics, telocentrics, and arms. *Paphiopedilum* subgenus *Brachypetalum*, *P.* section *Coryopedilum* and *P.* section *Pardalopetalum* have 26 metacentrics with two exceptions, but the arm number is constant. *Paphiopedilum* section *Cochlopetalum* has various numbers of telocentrics, and the arm number appears to be 50, but this needs to be confirmed by meiotic studies. Aside from *P. hookerae*, all species in section *Barbata* have various numbers of telocentrics. The arm number is 52, except for 56 in *P. hookerae* and 54 in *P. hennisianum.*

I have investigated 9 species from *P.* section *Barbata* and *P.* section *Cochlopetalum* (Table 5.3). Preparation methods for root tips were the same as those for *Phragmipedium.* Figure 5.2 shows idiograms for two species investigated. The chromosome numbers for 8 species agree with Karasawa as do the arm numbers of all four species which were determined. *Paphiopedilum wardii* (not seen by Karasawa) was found to have 44 chromosomes, which is the highest diploid number in *Paphiopedilum.* This does not agree with the counts by Duncan (1945), who reported variable numbers ranging from 41 to 45.

From Karasawa's data the total chromosome length and mean arm ratios (excluding telocentrics) in somatic tissues have been calculated (Table 5.2). Arm ratios from *Paphiopedilum* section *Cochlopetalum* were not calculated since the centromere position is uncertain. The mean chromosome lengths and arm ratios were also calculated for the six groups of *Paphiopedilum* (Table 5.4). *Paphiopedilum* section *Cochlopetalum* has the shortest chromosome lengths in the genus, while *P.* section *Barbata* has the longest. The brachypetalum group has the lowest arm ratios in *Paphiopedilum*, while the barbata and pardalopetalum groups have the highest.

COMPARISON OF KARYOLOGICAL DATA WITH THE CLADOGRAM

The occurrence of $2n = 20$ chromosomes among the plicate-leaved species suggests that their karyology is conservative relative to that of the conduplicate-leaved species. The common occurrence of $2n = 40$ among many Epidendroideae may indicate that the basal chromosome number of the orchid family is $2n = 20$ with the primarily epiphytic line having arisen from a paleotetraploid. I predict that *Selenipedium* will probably be found to have a chromosome number of $2n = 20$, since this number is so widespread among *Cypripedium*, *Criosanthes*, and *Phragmipedium.*

Within *Phragmipedium* the more primitive lorifolia group includes species with 20 somatic chromosomes, while both derived micropetalum and phragmipedium groups exhibit chromosomal repatterning. A decrease in chromosome number has apparently occurred in *P. boissierianum* if $2n = 20$ is primitive. *Phragmipedium* has the shortest total chromosome length known in the Cypripedioideae.

Within *Paphiopedilum* the basal chromosome number appears to be $2n = 26$ metacentrics with two sections having variable chromosome numbers accounted for by centric fissions. The most primitive group (section *Coryopedilum*) lacks telocentrics and has 26 metacentrics; the most derived group (section *Barbata*) contains a variable number of telocentrics. Centric fission appears to have occurred independently in the cochlopetalum group.

The somatic chromosome length is about twice that of *Phragmipedium* and about the same as for *Cypripedium.* Although the longest somatic chromosome length of the derived barbata group is consistent with the cladogram, the primitive coryopedilum group with the shortest is not. If asymmetrical karyotypes are derived, the barbata group has high arm ratios among the metacentrics, but these are exceeded by the more primitive pardalopetalum group.

If centric fissions have occurred in the barbata group, the question can be asked "do arm sizes of the metacentrics differ from those of the telocentrics in the same karyotype?" Differing arm sizes would imply that metacentrics which tend to undergo fission are larger or smaller than those which do not. Table 5.5 shows the mean arm length of metacentrics and telocentrics in 23 species from *Paphiopedilum* section *Barbata* (*P. fairieanum* does not belong in the section, and *P. hookerae* lacks telocentrics). In all cases the mean size of the telocentrics is larger than mean metacentric arm size. In only three species are the differences not significant. It would appear that the larger metacentrics tend to undergo centric fission more often than the smaller.

If fusions have also occurred in the barbata group, one might expect that the size of each member of a fusing telocentric pair would be random, and that asymmetry in the metacentric component would be manifested in higher arm ratios, which seems to be the case. *Paphiopedilum hookerae* has a higher mean arm ratio than all except two species of the $2n = 26$ groups. This may be accounted for by random centric fusions in a *P. bullenianum*-like ancestor.

There is little evidence for tandem growth of heterochromatin at the centromere or telocentrics as in mammals (Imai and Crozier, 1980). However, the extra arms of *P. hookerae* and *P. hennisianum* may have occurred by this mechanism. The latter species has one chromosome pair with a very short arm.

Chromosome number in the barbata group has little taxonomic utility, although high numbers are associated with certain complexes. However, the morphological similarity of *P. hookerae* ($2n = 28$) to *P. bullenianum* ($2n = 40$) and *P. callosum* ($2n = 32$) to *P. barbatum*($2n = 38$) shows that chromosome number per se is a poor indicator of relationships.

ANEUSOMATY AND POLYSOMATY IN THE CYPRIPEDIOIDEAE

There are several reports of variable chromosome numbers in somatic tissues of slipper orchids. Belling (1924) claims that he observed deficiencies of chromosomes in various cells of *Cyrpripedium acaule.* Duncan (1945) reported variable chromosome numbers in *Paphiopedilum wardii* from $2n = 41$ to $2n = 45$ and believed various chromosomes to be supernumerary. Chatterji (1966) noted polysomaty in *P. venustum* and stated that he had observed an occasional triploid cell based on $n = 19$. Vij and Mehra (1974) observed polyploid and aneuploid cells in *C. cordigerum.* In occasional preparations I have noted that occasional cells appeared to be polyploid, although the chromosome numbers were indeterminable. Although polysomaty may occur in roots of slipper orchids, I suggest that aneusomaty is accounted for by artificial effects of pretreatment.

POLYPLOIDY AND ANEUPLOIDY

Polyploidy is not an evolutionary mechanism in the slipper orchids (or apparently in most orchids) as it is in many vascular plants. Only two presumably wild-collected *Paphiopedilum* clones are polyploid. The first discovered polyploid is *P. insigne* 'Harefield Hall', a triploid (Mehlquist, 1947; Karasawa, 1978). The second case is a peculiar clone labeled *P. spicerianum* 'Marshall' which, unlike the normal species, has enormous flowers, a pubescent scape, and less violet and less contorted staminode (Atwood, 1980). The plant was found to have 43 chromosomes, of which only 8 were telocentric. In a normal triploid *P. spicerianum* 12 telocentrics would be expected among 45 chromosomes; however, the arm number (78) corresponds with the expected triploid arm number, and the total somatic chromosome length (259 μm) is close to that of the triploid *P. insigne* 'Harefield Hall' (243.2 μm, as determined from Karasawa's data). Since the flower exhibits the overwhelming influence of *P. spicerianum* and the plant has 8 telocentrics it was suggested that the plant had two genomes of *P. spicerianum* plus a third (13 metacentrics) from another source, perhaps from *P. insigne* with which it is sympatric. The single report of 30 somatic chromosomes in *C. guttatum* (Belaeva and Siplivinsky, 1976) may be a third example of polyploidy.

No other wild-collected plants are known to be polyploid. Since no wild tetraploids have been found, triploidy has probably arisen through nonreduction of gametes (Lenz, 1960; DeWet, 1979). This is most likely for the unusual *P. spicerianum* clone since a primary hybrid between *P. spicerianum* and *P. insigne* would be more likely to produce diploid gametes which, when fused with a reduced gamete of *P. spicerianum*, would produce a triploid zygote.

There are apparently no inherent cytological barriers to polyploidy as Lenz (1960) has shown that several complex hybrid cultivars are tetraploids. I suggest the reason that polyploidy is rare in slipper orchids is that the associated gigas qualities of the flowers upset the precise pollinator-labellum relationship so that pollination cannot occur. Since greatly enlarged flowers are horticulturally desirable, if polyploidy were common in wild populations, more polyploids should have been found.

Variable chromosome numbers are known in the conduplicate-leaved genera but not in the plicate-leaved genera. In *Paphiopedilum* the higher chromosome numbers are accounted for by centric fission, but in *Phragmipedium* the mechanism is not clear. Stebbins (1971, 1974) has indicated that aneuploids are associated with disturbed habitats, which may be true of weedy herbs of the temperate zone. It is not clear that *Paphiopedilum* section *Cochlopetalum* occurs in significantly different habitats from species with $2n = 26$ metacentrics. The non-aneuploid *Paphiopedilum* species occur on cliffs or tree crowns, which could be considered colonizing habitats. However, *P.* section *Barbata* occurs in the presumably more stable habitats of forest floors. It seems clear that variable chromosome numbers in the barbata group are associated with a "new" habitat, but it is most likely a less disturbed one. I suggest that chromosomal repatterning (of any sort, including aneuploid changes) may be associated with invasion of novel habitats, not merely disturbed ones.

CHAPTER VI: BIOGEOGRAPHY

To test a cladogram for its approximation to phylogeny is seemingly impossible without an extensive fossil record. However, if the patterns of relationship reveal additional patterns, the approximation is probably close. In this section I will show that the cladogram reveals two independent geographic patterns similar to the north-south morphological-geographical pattern of the *Selenipedium-Cypripedium* clade.

There is little evidence that orchids have recently migrated between the Asiatic and New World Tropics despite their easily dispersed seeds, and it is doubtful that the conduplicate-leaved genera attained their disjunct distributions by long distance dispersal. The very different karyologies and barriers to intergeneric hybridization imply that any long distance dispersal mechanism could only have operated very long ago, probably sufficiently long for a continuous distribution to have occurred. For these reasons I am assuming that *Paphiopedilum* and *Phragmipedium* have evolved from an ancient conduplicate-leaved group ("Protolorifolia") with relatively continuous distributions including both Old and New Worlds. Under a vicariance model it is not only possible to adumbrate the pathways of distribution but also to estimate the minimum time for divergence of the conduplicate-leaved genera.

ORIGIN OF THE CYPRIPEDIOIDEAE

Although most primitive slipper orchids now occur in South America, several facts seem peculiar if a South American origin is postulated. (1) There are no temperate slipper orchids in South America. (2) *Selenipedium* is not known from southern tropical South America. (3) The distribution of *Criosanthes* in the northern hemisphere is difficult to explain by a South American origin. (4) Most of the diversity of *Paphiopedilum* is found north of Wallace's Line, and only two species complexes are known for New Guinea. For a South American origin, the slipper orchids should have migrated northward approximately 5.7 m.y.B.P. (Raven and Axelrod, 1974) when the North and South American continents became joined. This might explain the origin of *Cypripedium*, but a tropical connection to Asia would be impossible within the last 6 million years. There is no evidence that slipper orchids ever occurred in Africa, Australia, New Zealand or adjacent islands, and if a continuous distribution of the conduplicate-leaved taxa ever occurred in the southern hemisphere, no relics have been found.

A Laurasian origin (as hypothesized for the Orchidaceae by Raven and Axelrod, 1974) is consistent with the above mentioned observations and the following facts. (1) The fossil record includes a continuous flora with presumably subtropical elements between western North America and Asia during mid-Miocene time (14-19 m.y.B.P.; Wolf, 1969). This would appear to be the most recent time that the conduplicate-leaved species could have had relatively continuous distributions. Post-Miocene cooling would have driven them southward, and generic distinction would have resulted from subsequent isolation. (2) As with the conduplicate-leaved genera a tropical connection between *Selenipedium* or "Protoselenipedium" and the Apostasioideae during the Miocene is possible. (3) Continuous distributions between North and South America have been possible only within the past 6 million years while a tropical connection between North America and Asia has not ocurred within the past 14 million years. This is interpreted as evidence that range extensions of the tropical genera via the Beringian area was the first event, which could have occurred only with a Laurasian origin. (4) The relatively low diversity of *Selenipedium* and *Phragmipedium* could be explained if the narrow connection between the North and South American continents restricted the number of species which could reach continental South America, although they may also be "poor evolvers." The high diversity of *Paphiopedilum* relative to that of *Phragmipedium* could be explained by the following two factors. (1) It has never passed through a narrow corridor as has *Phragmipedium.* (2) Fluctuating sea levels with the several Pleistocene glaciations may have caused alternate periods of isolation and recontact during which time hybridization could have occurred and new species formed. This idea first expressed by van Delden (1969) may explain how nearly half the species of *Paphiopedilum* occur in the barbata group, which includes plants of primarily forest habitats and not of relatively isolated limestone cliffs. Fluctuating sea levels would probably not have caused such dynamic changes in *Phragmipedium* or *Selenipedium* populations.

DISTRIBUTION PATTERNS

If the Cypripedioideae has a Laurasian origin, the tropical genera must have moved southward. *Paphiopedilum* could not have inhabited southeast Asian islands which arose largely since the Miocene. Similarly, *Phragmipedium* and *Selenipedium* doubtfully invaded South America prior to 6 m.y.B.P. (Raven and Axelrod, 1974; Schuster, 1976).

In *Paphiopedilum*, a southward migration route would first have followed mainland southeast Asia to the Malay Peninsula region to Sumatra, Java, Borneo, and lastly to the Philippines and New Guinea. The Luzon Strait region probably was never a major avenue for species migration since the waters are too deep for a continuous land mass to have formed. However, the region between Malaya, Java, and Borneo includes such shallow seas that even a modest change in sea level would expose vast expanses of land where populations could have expanded. The most primitive group (coryopedilum) is now restricted to the terminal portion of the migration route — the Philippines, Borneo, and New Guinea (Fig. 6.1). The cochlopetalum group occurs on Java and Sumatra (Fig. 6.1). The pardalopetalum group is widespread from southern China south to Malaya, east to Borneo, and the Philippines (Fig. 6.2). The paphiopedilum group is restricted to the Himalayan region with disjunct species in southern India and the Malay Peninsula (Fig. 6.1). The most derived group, barbata, encompasses most of the range of *Paphiopedilum* (Fig. 6.2). These ranges indicate that the more primitive *Paphiopedilum* groups now are either widespread or are located near the terminus of the hypothesized migration route, and that the more derived groups are either widespread or occur in the north where the genus has supposedly existed the longest. However, the greatest diversity of groups is found in the presumed areas of origin — northern Thailand and Burma (four groups) where the two most primitive groups are absent.

In *Phragmipedium* (Fig. 6.3) the most primitive section *(Lorifolia)* ranges from Costa Rica southward encompassing the entire South American range of *Phragmipedium.* The more primitive members of the lorifolia group lacking "horns" on the labellum and often having paniculate inflorescences occur on the eastern slopes of the Andes, eastward. The most derived sections occur in the region where *Phragmipedium* is hypothesized to have existed longest (Central and northeastern South America). The phragmipedium group ranges from Mexico south into Andean Peru but not eastward. The derived micropetalum group occurs in nothern Peru and eastern Colombia, very near where *Phragmipedium* must have invaded South America. All three groups occur in Colombia, and the lesser diversity in Central America is interpreted as an area effect.

The *Selenipedium-Cypripedium* clade exhibits a similar geographical-morphological pattern (Figs. 6.4, 6.5, 6.6) since the most primitive taxa (as

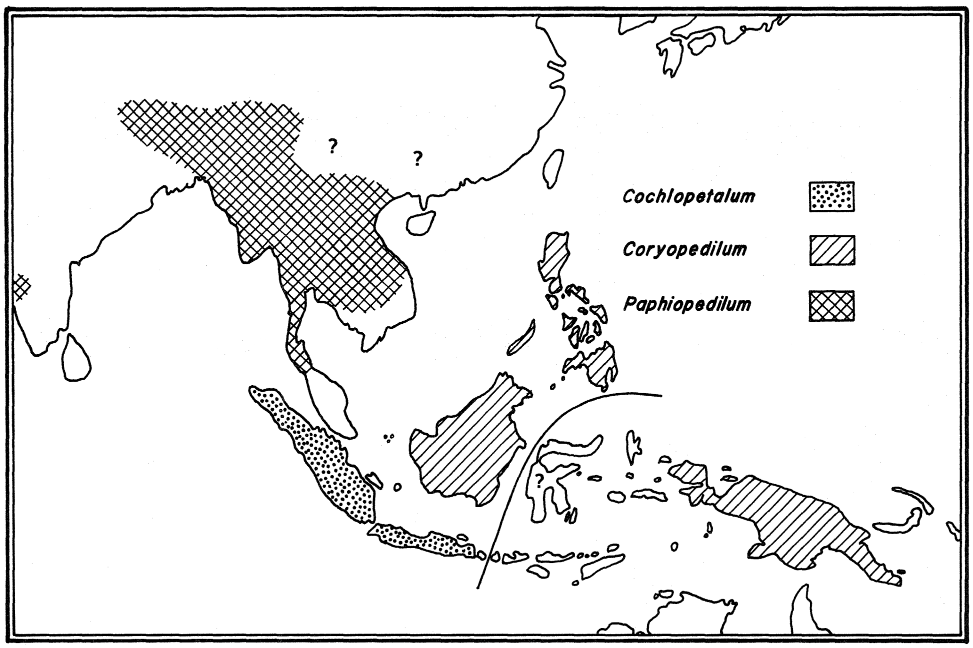

Fig. 6.1. Approximate maximum range limits of three sections of *Paphiopedilum.* This and the following maps serve to show relative positions of slipper orchid ranges. The line between Borneo and Celebes is Wallace's Line. Range limits for most *Paphiopedilum* groups are unknown in southern China. Section *Coryopedilum* may be represented on Celebes and adjacent islands, but its occurrence there is unknown. Under a vicariance model the disjunct species *P. druryi* (section *Paphiopedilum*) in southern India is accounted for by migration along mountains in eastern and southern India with subsequent extinction of ancestors.

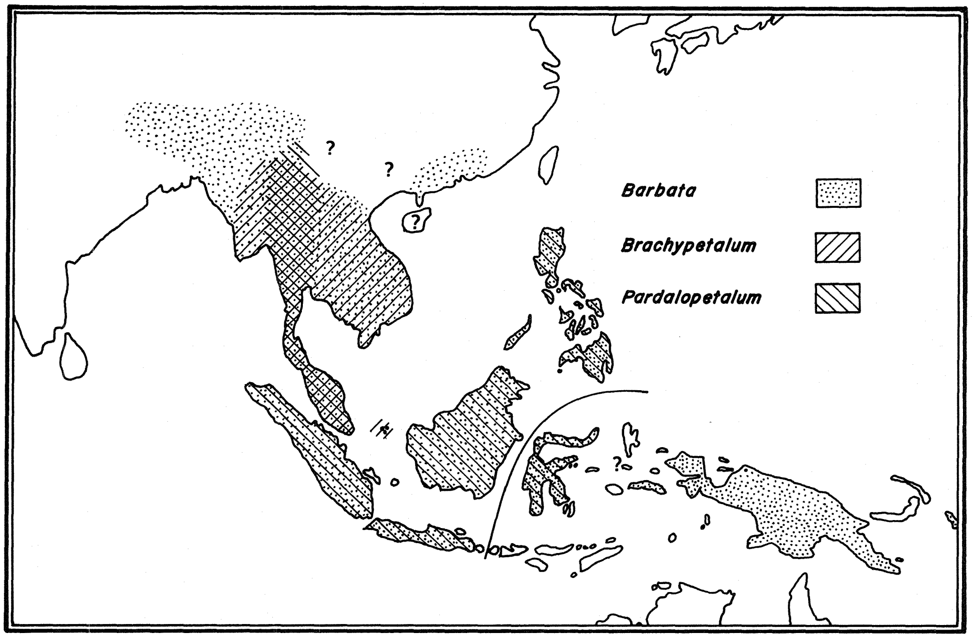

Fig. 6.2. Approximate range limits of *Paphiopedilum* sections *Barbata, Pardalopetalum,* and subgenus *Brachypetalum.* The line between Borneo and Celebes is Wallace's Line.

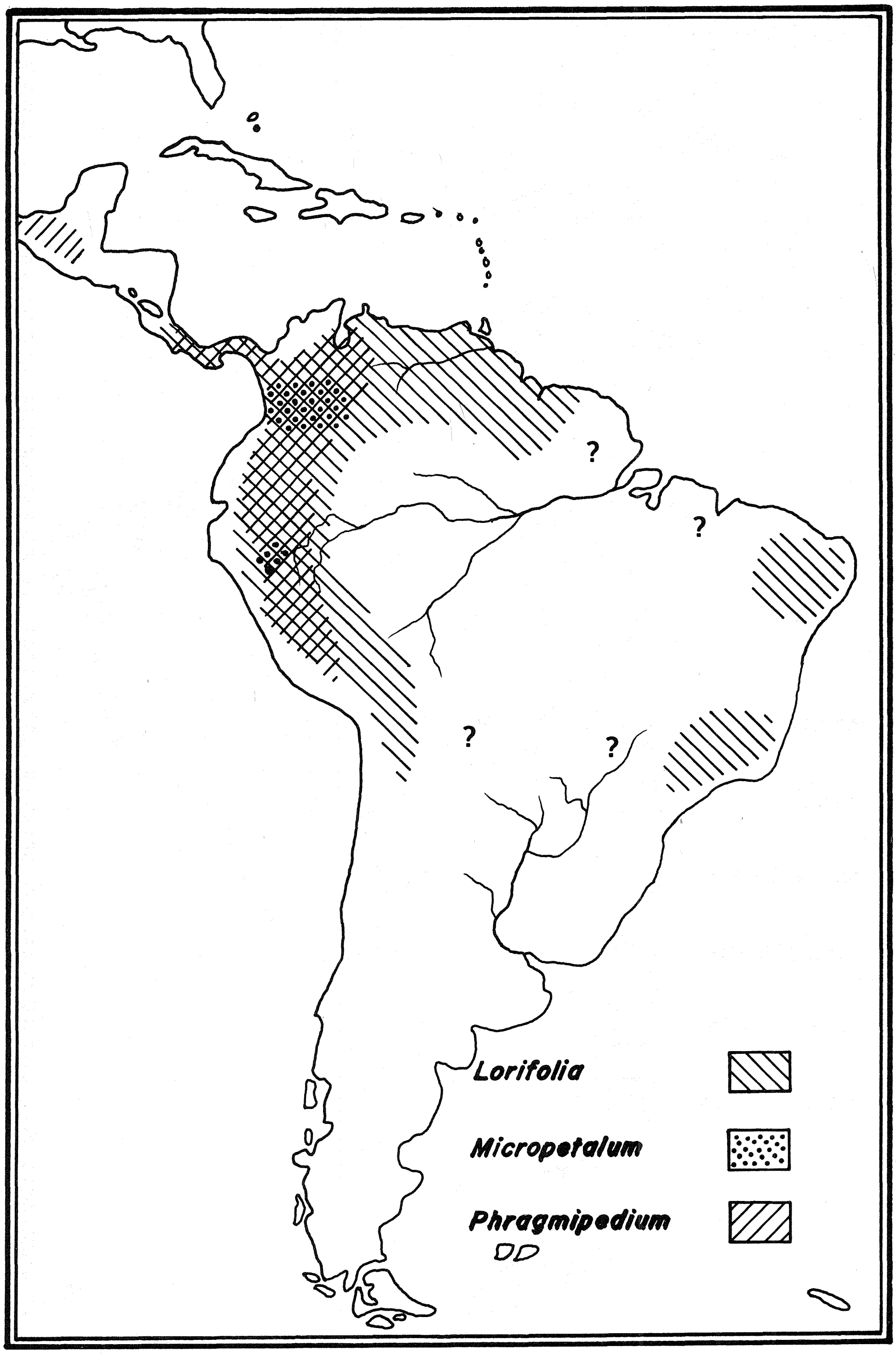

Fig. 6.3. Approximate range limits of the three *Phragmipedium* sections. Question marks indicate areas where species may occur or have occurred. There is little reason to believe that populations between the non-related east Brazilian species were ever continuous since each is closely related to species to the immediate west or northwest. Although *Phragmipedium* may have had more suitable habitats in the lower latitudes than *Selenipedium*, the presumed greater seed dispersibility probably accounts for its relatively broad range.

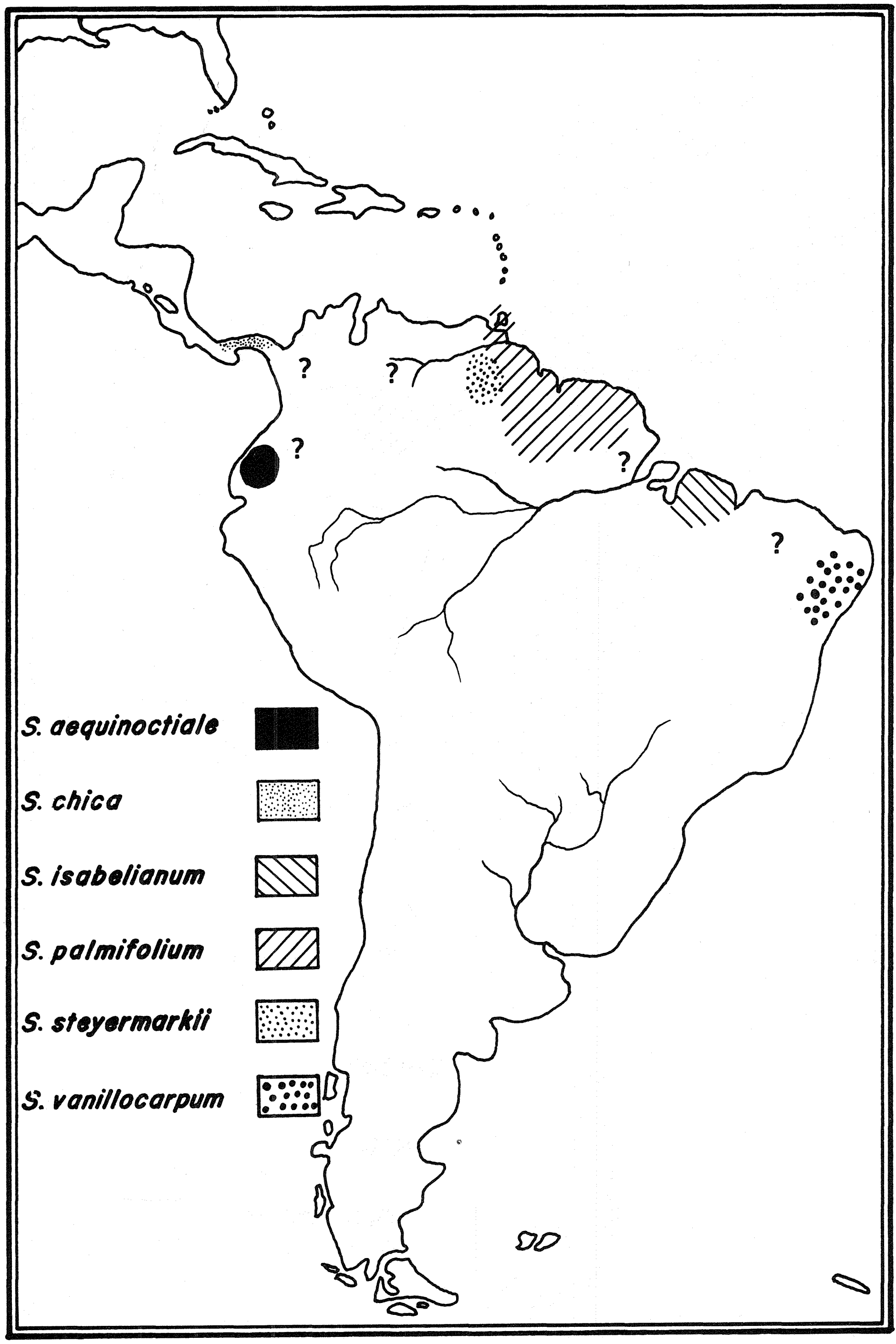

Fig. 6.4. The approximate range limits of *Selenipedium.* Question marks indicate locations where populations probably now occur or have occurred. Hoehne (1940) indicates that both *S. isabelianum* and *S. palmifolium* occur in Amazonas, but their extent is not clear. Note that *Selenipedium* is found primarily in northern tropical South America. The lack of reported occurrences in southern tropical South America is probably accounted for by the presumed lower dispersibility of the sclerotic seeds. It is conceivable that ranges have been increased by humans who cultivated the plants for their fruits.

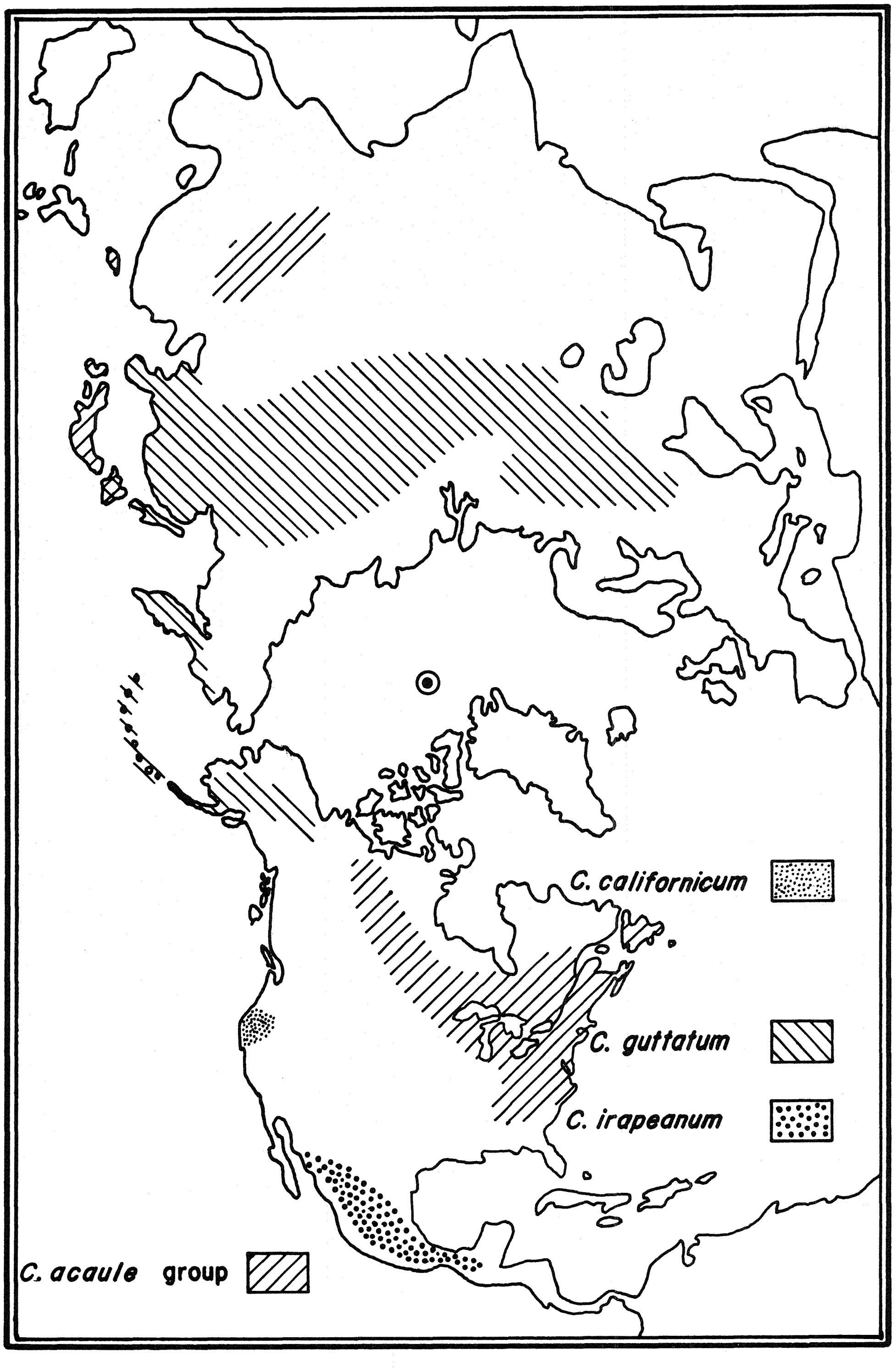

Fig. 6.5. Polar view of the northern hemisphere showing approximate range limits of three species of *Cypripedium* and the *C. acaule* group. The bull's-eye represents the North Pole. The *C. acaule* group as recognized here includes *C. japonicum*, *C. formosanum*, *C. cathayanum* and possibly *C. nutans*, and only *C. acaule* occurs in the New World.

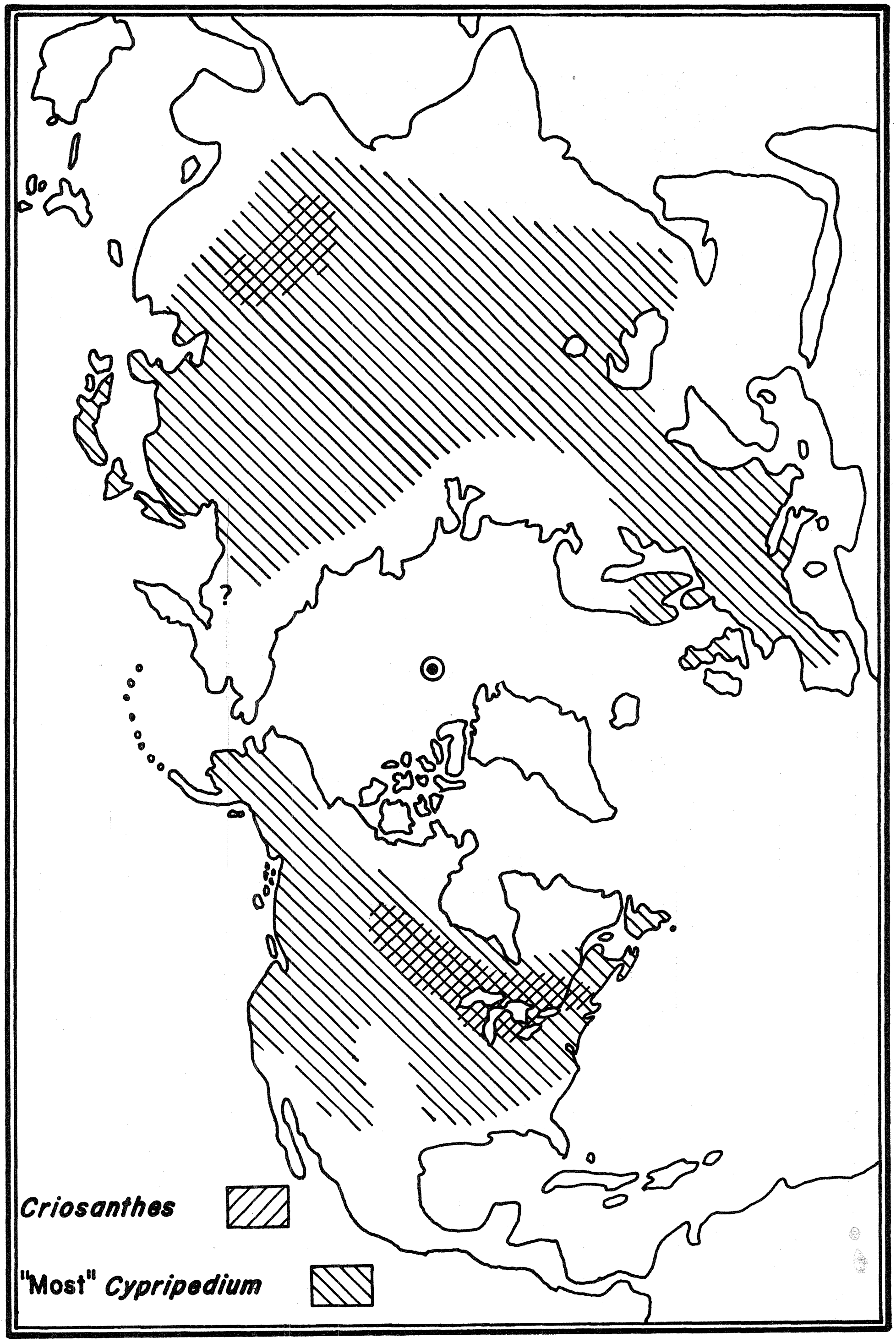

Fig. 6.6. The distribution of *Criosanthes* and "most" *Cypripedium* species not indicated in the preceding illustration. Under "most" *Cypripedium*, *C. fasciculatum*, *C. debile*, and *C. elegans* (Asiatic species) are included with *C. reginae*, the *C. calceolus* and *C. macranthum* complexes, although they are probably not related.

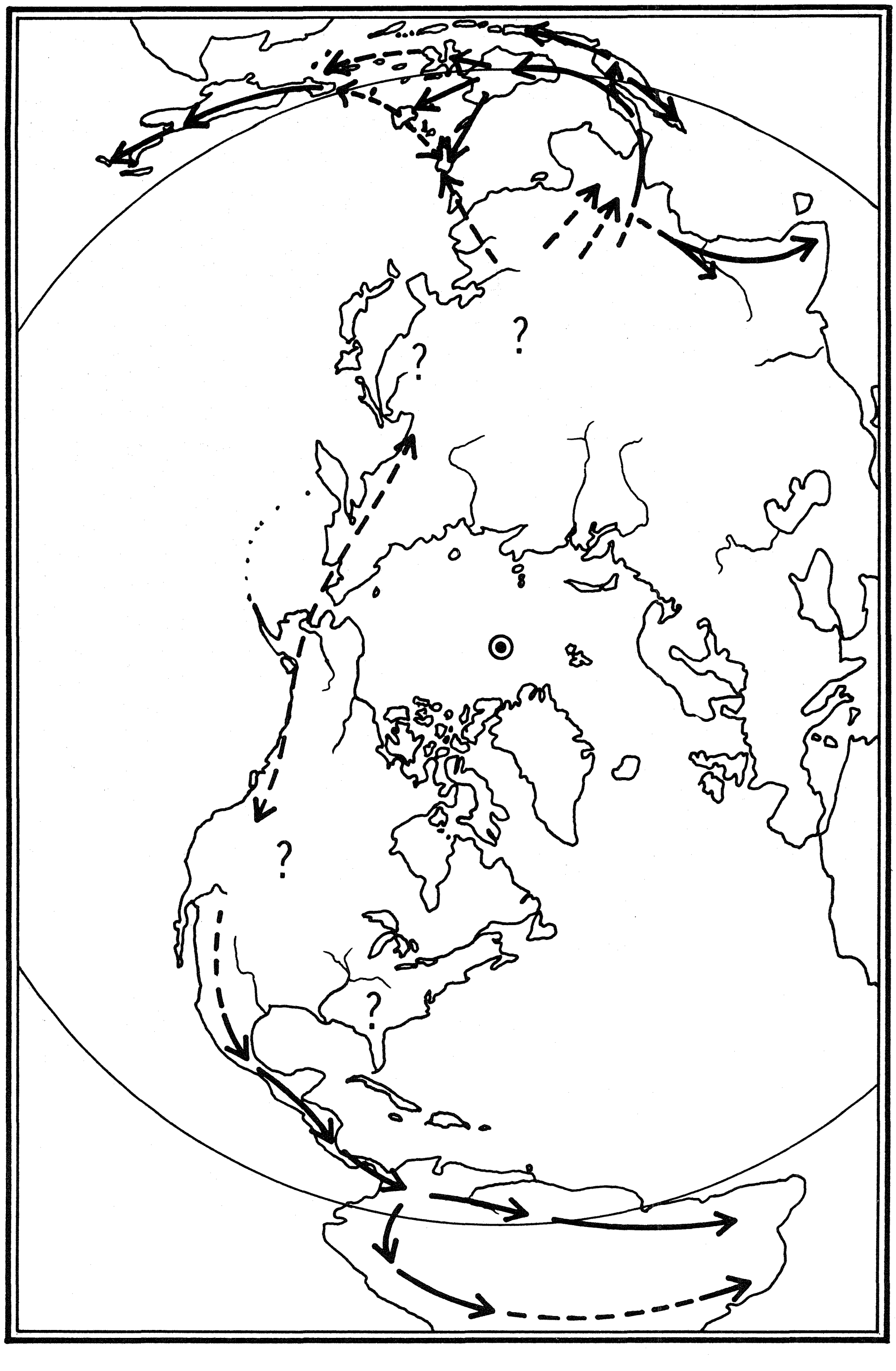

Fig. 6.7. North polar view of the distribution patterns of the tropical genera. The bull's-eye and circle represent the North Pole and Equator respectively. Question marks indicate areas where tropical slipper orchids probably occurred during the Miocene. The most derived species groups occur in areas where the first invasions probably occurred. Under this postulate, those species groups which are the most primitive are found in remote refugia, e.g., South America, Borneo, New Guinea, and the Philippines. The migration pathways for *Selenipedium* are similar to those for *Phragmipedium*, but the latter genus has become more widespread. The dashed line in the Beringian region represents the presumed continuous distributions of tropical species during Miocene time. The southward migration patterns are presumably accounted for by cooling of climates in the northern hemisphere since the Miocene.

determined by criteria mentioned earlier) now occur in the South American tropics, and the most derived are circumboreal.

The disjunct *Criosanthes arietina* and *C. plectrochila* are so similar that species distinction is questionable. The present distribution is interpreted as relictual, and the similarity probably indicates that the species are "poor evolvers."

The three distribution patterns with southerly distributions of the primitive taxa and greatest diversity in presumed areas of origin may be related to post-Miocene global cooling with southward movement or contraction of habitats in the northern hemisphere. Those species which colonized the more southerly habitats probably remained unchanged relative to those northern populations which were subjected to greater seasonal stress. Under this scenario the more southerly taxa would remain primitive and the northern derived in response to changing habitats. A very different biogeographic conclusion would have been necessary had only one of the three major groups been studied, since it would be of little concern that the coryopedilum and lorifolia groups are most closely related between the conduplicate-leaved genera, or that *Selenipedium* and the Apostasioideae appear to be related. This analysis suggests that the most primitive taxa may not only be absent from the center of origin, but may be very remote from it. Figure 6.7 illustrates probable migration patterns which were established since the Miocene.

This biogeographic scenario is speculative, but the three similar geographic patterns as revealed by cladistic analysis require explanation. Cooling climates with southward movement of habitats most similar to the ancestral ones is offered as a driving mechanism, although admittedly its effect should have decreased near the equator. If morphological-geographical patterns among other related angiosperms of the New and Old World Tropics are similar to those of the slipper orchids, the mechanism may offer at least a partial explanation for the accumulation of primitive taxa on the Asiatic Islands which have largely become exposed since the Oligocene.

CONCLUDING REMARKS

Both horticultural magazines and scientific journals have perpetuated a number of myths which have enshrouded the slipper orchids in mysticism. The prevailing belief is that the Cypripedioideae is a primitive and relic orchid group at an evolutionary dead end.

There is no evidence that the entire Cypripedioideae is primitive. The different staminal arrangement merely indicates that the subfamily diverged from other orchids very long ago. Although *Selenipedium* may be primitive, the patterns of diversity suggest that *Paphiopedilum* is very specialized.

There is no evidence that the Cypripedioideae is relic, with the exception of *Criosanthes.* For the slipper orchids to be relic, *Paphiopedilum* should not be as well developed in southeast Asia, nor should the many plicate-leaved species be so well represented over the northern hemisphere. True relics such as *Ginkgo*, *Metasequoia*, *Araucaria*, and the cycads are represented by few primitive species restricted in geographic area with singular or very disjunct ranges.

There is no evidence that the slipper orchids have reached an evolutionary dead end. The many species problems in *Paphiopedilum* section *Barbata* and the *Cypripedium calceolus* complex are probably extant examples of actively evolving groups. The small number of slipper orchid species relative to that of monandrous orchids may simply reflect lower speciation rates. This would be expected in a group of plants for which pollinator specificity is low, barriers to interspecific hybridization minimal, and floral variation adaptive. Despite prophecies of impending doom among the horticultural magazines, there is no reason to believe that the species are less numerous now than they have ever been. Although extinction of tropical species in North America by cooling climates may have occurred, it was doubtfully restricted to slipper orchids. However, the future outlook is less optimistic as destruction of tropical forests will have adverse effects on many populations, especially for *Paphiopedilum* section *Barbata.*

The interpretations of morphological and biogeographic patterns presented here may seem unorthodox, but I have approached the Cypripedioideae with the contention that slipper orchids are ordinary plants, albeit nice plants, subject to the same laws as other angiosperms. If this work stimulates botanists into seeking ways for presenting falsifiable hypotheses concerning their origin and evolution it shall have served its purpose.

ACKNOWLEDGMENTS

Gratitude is extended to Norris H. Williams, L. C. Anderson, F. C. James, M. Y. Menzel, and R. C. Dougherty for advice in their respective areas of expertise. I thank Calaway H. Dodson of the Missouri Botanical Gardens for enlightening conversations concerning pollination biology and R. L. Dressler of the Smithsonian Tropical Research Institute for stimulating conversations concerning the relationships and phylogeny of orchids.

Support from the American Orchid Society Fund for Education and Research for studying morphological and anatomical aspects of temperate orchids is much appreciated. I also wish to express appreciation for funds from The Florida State University and Sigma Xi for enabling me to study *Phragmipedium longifolium* in Panama.

LITERATURE CITED

Abe, K. 1972. Contributions to the embryology of the family Orchidaceae VII. A comparative study of the orchid embryo sac. Sci. Rep. Tohoku Imp. Univ., Ser. 4, Biol. 36 (3): 179-201.

Adams, H. 1959. Aspects of Variation in the Orchidaceae. *In* C. L. Withner, (ed.), The Orchids: A Scientific Survey. The Ronald Press Company, New York. 648 pp.

Ames, O. 1932. Insect visitors to *Cypripedium parviflorum.* Amer. Orchid Soc. Bull. 1: 91.

Andre, E. 1875. Les Cypripediums Vénéneux. Ill. Hort. 22: 114-115.

Anonymous. 1913. *Selenocypripedium malhouitri.* Orchid Rev. 21: 79.

——. 1944. *Cypripedium californicum.* Orchid Rev. 52: 83.

Arditti, J., Michaud, J. D., and Healey, P. L. 1979. Morphometry of orchid seeds I. *Paphiopedilum* and native California and related species of *Cypripedium.* Amer. J. Bot. 66 (10): 1128-1137.

Atwood, J. T. 1980. The identification of an unusual *Paphiopedilum.* Amer. Orchid Soc. Bull. 49 (2): 127-130.

Atwood, J. T. and Williams, N. H. 1978. The utility of epidermal cell features in *Phragmipedium* and *Paphiopedilum* (Orchidaceae) for determining sterile specimens. Selbyana 2 (4): 356-366.

——. 1979. Surface features of the adaxial epidermis in the conduplicate-leaved Cypripedioideae (Orchidaceae). Bot. J. Linn. Soc. 78: 141-156.

Barthlott, W. 1976. Morphologie der Samen von Orchideen in Hinblick auf taxonomische und functionelle Aspekte. Pp. 444-455 *in* Proc. 8th World Orchid Conference (Frankfurt).

Belaeva, V. A. and Siplivinsky, V. N. 1976. Chromosome numbers and taxonomy of some species of Baikal flora II (in Russian). Bot. Zurn. (Moscow and Leningrad) 61 (6): 873-880.

Belling, J. 1924. Detachment (elimination) of chromosomes in *Cypripedium acaule.* Bot. Gaz. (London) 78: 458-460.

Bentham, G. and Hooker, J. 1883. Genera Plantarum 3 (2): 634-635.

Blume, K. L. 1858. Flora Javae (n.s.), pp. 139-143. Amsterdam.

Boissier, E. 1884. Flora Orientalis 5: 94. Geneva and Basil.

Brieger, F. G. 1969. Patterns of evolutionary and geographical distribution of neotropical orchids. Biol. J. Linn. Soc. 1: 197-217.

——. 1971. Unterfamilie Cypripedioideae. Pp. 161-198 *in* R. Schlechter, Die Orchideen (Revised edition).

Catesby, M. 1771. The Natural History of Carolina, Florida and the Bahama Islands.

Catling, P. M. 1980. Autogamy in north-eastern North American orchids. (Abstr.) Botanical Society of America Miscellaneous Series Publication 158: 20.

Catling, P. M. and Knerer, G. 1980. Pollination of the small white lady's-slipper *(Cypripedium candidum)* in Lambton County, southern Ontario. Canad. Field-Naturalist 94 (4): 435-438.

Chatterji, A. K. 1966. Polysomaty in orchids. Naturwissenschaften 53: 509-510.

Correll, D. S. 1950. Native orchids of North America. Chronica Botanica Co., Waltham, Mass. 399 pp.

Crane, F. H. 1931. Flowers and folklore from far Korea. The Sanseido Co., Ltd. Tokyo, Osaka. 93 pp.

Crisci, J. V. and Stuessy, T. F. 1980. Determining primitive character states for phylogenetic reconstruction. Systematic Botany 5 (2): 112-135.

Curtis, S. and Hooker, W. J. 1829. *Cypripedium macranthon.* Large-flowered lady's slipper. Bot. Mag. 56: Tab. 2938.

Curtis, W. 1792. *Cypripedium album,* white-petal'd ladies slipper. Bot. Mag. 5: Tab. 216.

Darwin, C. 1885. The Various Contrivances by which Orchids are Fertilized by Insects, pp. 226-246. William Clowes & Sons, Ltd. London.

Davis, G. L. 1966. Systematic embryology of the angiosperms, pp. 194-196. John Wiley and Sons, Inc. New York.

Daumann, E. 1968. Zur Bestäubungökologie von *Cypripedium calceolus* L. Österr. Bot. Z. 115: 434-446.

Day, C., Jr. 1972. Observations of self-pollination in *Paphiopedilum* species. Amer. Orchid Soc. Bull. 41: 592.

Desbois, F. 1888. Monographie des *Cypripedium, Selenipedium* et *Uropedium.* Librairie centrale d'agriculture, Paris. 159 pp.

DeWet, J. M. J. 1979. Origins of polyploids. Pp. 3-15 *in* W. Lewis (ed.), Polyploidy. Plenum Press, New York.

Dodson, C. H. 1966. *Cypripedium, Phragmipedium* and allied genera. Amer. Orchid Soc. Bull. 35: 125-128.

Dressler, R. D. 1981. The Orchids: Natural History and Classification. Harvard University Press, Cambridge, Mass. 352 pp.

Dressler, R. L. and Dodson, C. H. 1960. Classification and phylogeny in the Orchidaceae. Ann. Missouri Bot. Gard. 47: 25-68.

Duncan, R. E. 1945. Production of variable aneuploid numbers of chromosomes within the root tips of *Paphiopedilum wardii.* Amer. J. Bot. 32: 506-509.

——. 1947. The hybrid lady slipper. Orchid Digest. 11: 199-207.

——. 1959. List of chromosome numbers in orchids. Pp. 529-587 *in* C. Withner (ed.), The Orchids: A Scientific Survey. The Ronald Press Co., New York.

Duncan, R. E. and MacLeod, R. A. 1948a. Chromosomes of the *Brachypetalums*. Amer. Orchid Soc. Bull. 17: 170-174.

——. 1948b. Chromosomes of the insigne complex of lady-slippers. Amer. Orchid Soc. Bull. 17: 424-429.

——. 1949a. The chromosomes of the continental species of *Paphiopedilum* with solid green leaves. Amer. Orchid Soc. Bull. 18: 84-89.

——. 1949b. The chromosomes of some of the *Polyantha*. Amer. Orchid Soc. Bull. 18: 159-163.

——. 1949c. The chromosomes of the species of *Cochlopetalum* Hallier. Amer. Orchid Soc. Bull. 18: 573-576.

——. 1950a. The chromosomes of *Eremantha tesselata*. Amer. Orchid Soc. Bull. 19: 137-142.

——. 1950b. The chromosomes of *Paphiopedilum sublaeve*. Amer. Orchid Soc. Bull. 19: 489-492.

Dunsterville, G. C. K. 1970. *Phragmipedium klotzscheanum* (Rchb. f. ex Schomb.) Rolfe. Orchid Rev. 78: 292-294.

Dunsterville, G. C. K. and Dunsterville, E. 1980. *Selenipedium steyermarkii* — a "commodious" orchid. Amer. Orchid Soc. Bull. 49 (11): 1225-1229.

Dunsterville G. C. K. and Garay, L. 1963. Venezuelan Orchids. Orchid Rev. 71: 384-387, 410.

Francini, E. 1934. Ibridazione interspecifica nel genere "*Paphiopedilum*". Nuovo Giornale Botanico Italiano (n.s.) 41 (2): 189-237.

Garay, L. A. 1960. On the origin of the Orchidaceae. Bot. Mus. Leafl. 19 (3): 57-96.

——. 1972. On the origin of the Orchidaceae II. J. Arnold Arbor. 53 (2): 202-215.

——. 1978. Orchidaceae. Pp. 14-23 *in* G. Harling and B. Sparre, Flora of Ecuador 9.

——. 1979. The Genus *Phragmipedium*. Orchid Digest 43 (4): 133-148.

Gardener's Chronicle 11: 394 (1892).

Gerard, J. 1597. The Herball. Theatrum orbis terrarum, Ltd. Amsterdam. 303 pp. Reprinted by Walter J. Johnson, Inc. 1974.

Gorinsky, P. 1972. Habitat notes from a collection in Guyana of *Phragmipedium klotzscheanum*. Orchid Digest 36: 151-154.

Goulandris, N. A., Goulimis, C. N. and Stearn, W. T. (ed.) 1968. Wild Flowers of Greece. J. Makris S. A. Kifissias 32, Amaroussion-Athens. 206 pp.

Guignard, J. A. 1886. Insects and Orchids. Ann. Rep. Ent. Soc. Ontario 16: 39-48.

Hallier, H. 1897. Über *Paphiopedilum amabile* und die Hochgebirgsflora des Berges K'Lamm in Westborneo nebst einer Übersicht über die Gattung *Paphiopedilum*. Ann. Jar. Bot. Buitenzorg. 14: 18-52.

Hardegger E., Schellenbaum, M., and Corrodi, H. 1963. Über induzierte Abwehrstoffe bei Orchideen II. Helv. Chim. Acta 46 (2): 1171-1180.

Heinrich, B. 1975. Bee flowers: a hypothesis on flower variety and blooming times. Evolution: 29: 325-334.

Hoehne, F. C. 1940. Flora Brasilica 12: Orchidaceas, pp. 40-50, Romiti and Lanzara, Sao Paulo, Brazil.

——. 1949. Iconografia de Orchidaceas do Brasil. Printed by S. A. Industries Graphicars, F. Lanzara. Sao Paulo, Brasil. 301 pp.

Hoffmann, K. M. 1929. Cytologische Studien bei den Orchidaceen. Ber. Deutsch. Bot. Ges. 47: 321-326.

——. 1930. Beiträge zur Cytologie der Orchidaceen. Planta 10: 523-595.

Hooker, J. D. 1891. *Cypripedium californicum*. Bot. Mag. 117: Tab. 7188.

——. 1893, *Cypripedium fasciculatum* var. *pusillum*. Bot. Mag. 119: Tab. 7275.

House, H. D. 1905. Further notes on the orchids of central New York. Bull. Torry Bot. Club 32: 373-382.

Humphrey, L. M. 1932. The somatic chromosomes of eight species of Orchidaceae. Proc. Iowa Acad. Sci. 39: 137.

Hurst, C. C. 1925. Experiments in genetics. Cambridge Press, Great Britain. 578 pp.

Imai, H. T. and Crozier, R. H. 1980. Quantitative analysis of directionality in mammalian karyotype evolution. Amer. Naturalist 116 (4): 537-569.

Johnson, L. 1884. A Manual of the Medical Botany of North America. William Wood and Co., New York. 292 pp.

Kamemoto, H., Sagarik, R. and Dieutrakul, S. 1963. Karyotypes of *Paphiopedilum* species of Thailand. The Kasetsart Journal 3 (2): 64-78.

Karasawa, K. 1978. Karyomorphological studies on the intraspecific variation of *Paphiopedilum insigne*. Kromosomo 2 (9): 233-255.

——. 1979. Karyomorphological studies in *Paphiopedilum*, Orchidaceae. Bulletin of the Hiroshima Botanical Garden 2: 1-149.

Karasawa, K. and Tanaka, R. 1976. Chromosome Information Service 20: 13-14.

Kipping, J. L. 1971. Pollination studies of native Orchids. Thesis. San Francisco State College.

Knuth, P. 1909. Handbook of Flower Pollination. Clarendon Press, Oxford. 644 pp.

Kraenzlin, F. 1897. Orchidacearum Genera et Species I. Mayer and Müller, Berlin. Reprinted by Verlag von J. Cramer, S-H Service Agency, Inc., New York. 1969.

Lavarack, P. S. 1971. The taxonomic affinities of the Neottiodeae. Thesis. University of Queensland.

Lenz, L. W. 1960. The cytology of the white cypripediums. Amer. Orchid Soc. Bull. 29 (3): 187-192.

Lindley, J. 1840. Genera and Species of Orchidaceous Plants. Ridgeways, Picadilly, London. Pp. 525-532.

——. 1846. Orchidaceae Lindenianae. Bradbury and Evans, London. 28 pp.

Linnaeus, C. 1753. Species Plantarum. Impensis Laurentii Salvii, Stockholm. 1200 pp.

L'obel, M. de. 1576. Plantum sev stirpium historia. C. Plantini, Antwerp. 2 vols.

Love, A. and Simon, W. 1968. Cytotaxonomical notes on some American orchids. Southw. Naturalist 13: 335-342.

Luer, C. 1975. The Native Orchids of the United States and Canada excluding Florida. W. S. Cowell, Ltd., Ipswich, England. 361 pp.

MacDougal, D. T. 1894. On the poisonous influence of *Cypripedium spectabile* and *Cypripedium pubescens*. Minnesota Bot. Stud. 1: 32-36.

McQuade, H. 1949. The cytology of *Paphiopedilum maudiae* Hort. Ann. Missouri Bot. Gard. 36: 433-474.

Mammen, V. and Mammen, J. 1974. Rediscovering *Paphiopedilum druryi* in southern India. Orchid Digest 38: 31-36.

Mehlquist, G. A. 1947. Polyploidy in the genus *Paphiopedilum* Pfitz. (*Cypripedium* Hort.), and its practical implications. Missouri Bot. Gard. Bull. 35: 211-233.

Mehra, P. N. and Bawa, K. S. 1970. Cytological observations on some northwest Himalayan orchids. Caryologia 23 (3): 273-282.

Mulay, B. N. and Panikkar, T. K. B. 1953. The chromosome number and morphology in *Cypripedium speciosum* L. Proc. Rajasthan Acad. Sci. 4: 29-31.

Newhouse, C. 1976. Pollination biology in seven taxa of Michigan Orchidaceae and a study of *Cypripedium calceolus* in Michigan based on living plants and herbarium specimens. Thesis. Michigan State University. 98 pp.

Newton, G. D. and Williams, N. H. 1978. Pollen morphology of the Cypripedioideae and the Apostasioideae (Orchidaceae). Selbyana 2: 169-182.

Nilsson, L. A. 1979. Anthecological studies on the lady's slipper, *Cypripedium calceolus* (Orchidaceae). Bot. Notiser 132: 329-347.

Pace, L. 1907. Fertilization in *Cypripedium*. Bot. Gaz. (Crawfordsville) 44: 353-374.

Parkinson, J. 1640. Theatricum Botanicum, the Theater of Plants or An Universall and Compleate Herball, p. 217. Thomas Cotes, London.

Pfitzer, E. H. H. 1886. Morphologische Studien Über die Orchideenblüthe. C. Winter's Universitätsbuchhandlung, Heidelberg. 139 pp.

——. 1888. Die Orchideen. *In* A. Engler and K. Prantl (eds.), Die Natürlichen Pflanzenfamilien 2: 52-96.

——. 1894. Beiträge zur Systematik der Orchideen. Bot. Jahrb. Syst. 19: 1-42.

——. Orchidaceae-Pleonandrae. *In* Engler, E. (ed.), Das Pflanzenreich 12. Reprinted in 1957 by Verlag von H. R. Engelmann (J. Cramer). Weinheim/Bergstr.

Porcher, F. P. 1863. Resources of the Southern Fields and Forests. Evans and Cogwell, Charleston. 601 pp.

Raffill, C. D. 1913. Bee visiting *Cypripedium reginae.* Orchid Rev. 21: 248.

Rafinesque, C.S. 1818. Flora Americae Septentrionalis, or a systematic arrangement and description of the plants of North America. Amer. Monthly Mag. and Crit. Rev. 2: 268.

——. 1828. Medical flora 1. Atkinson and Alexander, Philadelphia. 268 pp.

——. 1836. Flora Telluriana 4: 45-47. H. Probasco, Philadelphia.

Rao, V. S. 1974. The relationships of the Apostasiaceae on the basis of floral anatomy. J. Linn Soc., Bot. 68: 319-327.

Raven, P. H. and Axelrod, D. I. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61(3): 539-673.

Reichenbach, H. G. 1854. Xenia Orchidaceae 1: 3.

Rolfe, R. A. 1888. Bigeneric Orchid Hybrids. J. Linn. Soc., Bot. 24: 156-170.

—— (ed.). 1894a. *Cypripedium spectabile* and *C. pubescens* as poisonous plants. Orchid Rev. 2: 141-142.

—— (ed.). 1894b. Note appended after W. Swan, Hybrid between *Cypripedium* and *Selenipedium.* Orchid Rev. 2: 171.

——. 1895. *Cypripedium* X *corndeanii.* Orchid Rev. 3: 215.

——. 1896. The *Cypripedium* group. Orchid Rev. 4: 327-334, 363-367.

——. 1901. The *Cypripedium* group. Orchid Rev. 9: 175.

——. 1912. Our note book. Orchid Rev. 20: 2.

Rosso, S. W. 1966. The vegetative anatomy of the Cypripedioideae (Orchidaceae). J. Linn. Soc., Bot. 59: 309-341.

Sanders, St. Albans. 1947. Complete List of Orchid Hybrids. Gibbs and Bamforth Ltd., St. Albans, Great Britain. 308 pp.

Schlechter, R. 1926. Das System der Orchideen. Notizbl. Bot. Gart. Berlin-Dahlem 9 (88): 563-591.

Schmalle, H. and Hausen, B. M. 1979. A New Sensitizing Quinone from Lady Slipper *(Cypripedium calceolus).* Naturwissenschaften 66: 527-528.

Schmid, R. and Schmid, J. 1977. Fossil History of the Orchidaceae. Pp. 25-45 *In* J. Arditti (ed.), Orchid Biology. Cornell University Press, Ithaca, New York.

Schuster, R. M. 1976. Plate Tectonics and its Bearing on the Geographical Origin and Dispersal of Angiosperms. Pp. 48-138 *in* Beck, C. B. Origin and Early Evolution of Angiosperms. Columbia University Press, New York.

Solereder, H. and Meyer, F. J. 1930. Systematische Anatomie der Monokotyledonen 6. Scitamineae-Microspermae (Orchidaceae) Berlin: Verlag von Gebrüder Bornträger. English translation, 1969. Jerusalem: Israel Program for Scientific Translations.

Stafleu, F. A. (ed.). 1978. International Code of Botanical Nomenclature. Bohn, Scheltema, and Halkema, Utrecht. 457 pp.

Stebbins, G. L. 1971. Chromosomal Evolution in Higher Plants. Addison-Wesley Publishing Company, Reading, Mass. 216 pp.

——. 1974. Flowering Plants. Belknap Press, Harvard University, Cambridge, Mass. 399 pp.

Stein, B. 1892. Stein's Orchideenbuch. Paul Parey, Berlin. Pp. 175-191.

Stevens, P. F. 1980. Evolutionary polarity of character states. Ann. Rev. Ecol. Syst. 11: 333-358.

Stoutamire, W. P. 1967. Flower biology of the lady's-slippers. The Michigan Bot. 6: 159-175.

Swamy, B. G. L. 1948. Vascular anatomy of orchid flowers. Bot. Mus. Leafl. 13: 61-95.

Swan, W. 1894. Hybrids between *Cypripedium* and *Selenipedium.* Orchid Rev. 2: 171.

Swanson, E. S., Cunningham, W. P. and Holman, R. T. 1980. Ultrastructure of glandular ovarian trichomes of *Cypripedium calceolus* and *C. reginae* (Orchidaceae). Amer. J. Bot. 67 (5): 784-789.

Swartz, O. 1800. Kongl. Vetensk. Acad. Nya Handl. 21: 115-138.

Swinburne, T. W. 1896. Hybrids between *Cypripedium* and *Selenipedium.* Orchid. Rev. 4: 318.

Tanaka, R. and Kamemoto, H. 1974. List of chromosome numbers in species of the Orchidaceae. Pp. 411-483 *in* C. L. Withner (ed.), The Orchids: Scientific Studies. John Wiley and Sons, New York.

Urech, J., Fechtig, B., Nuesch, J. and Vischer, E. 1963. Hircinol, eine antifungisch wirksame Substanz aus Knollen von *Loroglossum hircinum* (L.) Rich. Helv. Chim. Acta 46 (3): 2758-2766.

Van Delden, R. J. 1969. Notes regarding the evolution of the genus *Paphiopedilum* in the latest glacial epoch. Orchid Digest 33 (5): 151-154.

Van der Pjil, L. and Dodson, C.H. 1966. Orchid Flowers: Their Pollination and Evolution. University of Miami Press, Coral Gables, Florida. 214 pp.

Veitch, J. and Sons. 1889. Tribe Cypripedieae *in* A Manual of Orchidaceous Plants, 2 (4): 1-108. Reprinted by A. Asher and Co., Amsterdam. 1963.

Vermeulen, P. 1966. The system of the Orchidales. Acta Botanica Neerl. 15: 224-253.

Vij, S. P. and Gupta, G. C. 1976. Cytological investigations into W. Himalayan Orchidaceae I. Chromosome numbers and karyotypes of taxa from Kashmir. Cytologia 40 (3-4): 613-621.

Vij S. P. and Mehra, P. N. 1974. Cytological studies in the east Himalayan Orchidaceae III: Cypripedieae. Caryologia 27 (3): 293-300.

Vogel, S. 1962. Duftdrusen im Dienste der Bestäubung. Abh. Math.-Natur. Kl. Akad., Mainz 10: 601-763.

Wagner, W. H., Jr. 1980. Origin and philosophy of the groundplan-divergence method of cladistics. Systematic Botany 5: 173-193.

Walker, E. P. (principal author), Warnick, F., Lange, K. I., Uible, H. F., Hamlet, S. E., Davis, M. A., Wright, P. F. 1975. Mammals of the World (2 vols.) Third revised edition by J. L. Paradiso. The Johns Hopkins University Press. Baltimore and London. 1500 pp.

Weibel, R. 1945. La placentation chez les Tiliacée. Candollea 10: 155-177.

Whiffin, T. and Bierner, M. W. 1972. A quick method for computing Wagner trees. Taxon 21: 83-90.

Williams. B. S. and Williams, H. 1894. The Orchid Grower's Manual. Published at Victoria and Paradise Nurseries, Upper Holloway, London. 796 pp.

Williams, N. H. 1975. Stomatal development in *Ludisia discolor* (Orchidaceae): mesoperigenous subsidiary cells in the monocotyledons. Taxon 24: 281-288.

——. 1976. Subsidiary cell development in the Catasetinae (Orchidaceae) and related groups. J. Linn. Soc., Bot. 72: 299-309.

——. 1979. Subsidiary cells in the Orchidaceae: their general distribution with special reference to development in the Oncidieae. J. Linn. Soc., Bot. 78: 41-66.

Wilson, W. W. 1961. *Selenocypripedium* confusion. Amer. Orch. Soc. Bull. 30: 806-807.

Wolfe, J. A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madroño 20: 83-110.

Wood, M. W. 1976. *Paphiopedilum victoria-regina.* Orchid Rev. 84: 133-143.

Ziegler, B. 1981. Mikromorphologie der Orchidaceen-Samen unter berücksichtigung taxonomisches Aspekte. A Thesis. Ruprecht Karls Universität, Heidelberg.

Zoller, H. (ed.) 1976. Conradi Gesneri Historia Plantarum 4: 16-17, Facsimile by K. Gesner, 1541 included. Urs Graf Verlag, Dietikon, Zürich.

APPENDICES

In Appendices 1-8, names recognized here follow the equal signs (=) in cases of synonymy. Names followed by "group" or "subgroup" lack designated taxonomic status and are not italicized. The species lists are for comparison of classifications only, and author names have been standardized so that comparison is facilitated.

Appendix 1. Classification of the Cypripedioideae (Cypripedeae) according to Lindley (1840).

1. Foliosa group (stems many-leaved; lateral sepals connate to the apex)
    - *Cypripedium candidum* Muhlenb. ex Willd.
    - *C. molle* Lindl. = *C. irapeanum* Llave & Lex.
    - *C. palmifolium* Lindl. = *Selenipedium palmifolium* (Lindl.) Rchb. f.
    - *C. parviflorum* Salisb.
    - *C. pubescens* Willd.
    - *C. spectabile* Sw. = *C. reginae* Walt.
2. Foliosa group (stems many-leaved but lateral sepals free at apex)
    - *C. calceolus* L.
    - *C. cordigerum* D. Don
    - *C. irapeanum* Llave & Lex.
    - *C. macranthum* Sw.
    - *C. montanum* Dougl. ex Lindl.
    - *C. passerinum* Richards
    - *C. ventricosum* Sw.
3. Arietinium (sic) group (stems many-leaved, lateral sepals totally free)
    - *C. arietinum* R. Br.
4. Bifolia (stems two-leaved)
    - *C. guttatum* Sw.
    - *C. japonicum* Thunb.
5. Acaulia (all leaves basal)
    - *C. humile* Salisb. = *C. acaule* Mich.
    - *C. insigne* Wall. ex Lindl. = *Paphiopedilum insigne* (Wall. ex Lindl.) Pfitz.
    - *C. lindleyanum* Schomb. ex Lindl. = *Phragmipedium lindleyanum* (Schomb. ex Lindl.) Rolfe
    - *C. purpuratum* Lindl. = *Paphiopedilum purpuratum* (Lindl.) Stein
    - *C. venustum* Wall. ex Sims = *Paphiopedilum venustum* (Wall. ex Sims) Pfitz.

(Section unknown)
- *C. caudatum* Lindl. = *Phragmipedium caudatum* (Lindl.) Rolfe

Appendix 2. Classification of the Cypripedioideae (Diandrae-Cypripedilinae) according to Pfitzer (1888). Three genera recognized.

1. *Cypripedilum* L. = *Cypripedium* L. (leaf vernation convolute, testa thin)
    - a. Arietina group (lateral sepals free)
        - *C. arietinum* R. Br.
    - b. Foliosa group (lateral sepals fused, foliage leaves several)
        - *C. acaule* Ait.
        - *C. calceolus* L.
        - *C. guttatum* Sw.
        - *C. macranthum* Sw.
        - *C. pubescens* Willd.
        - *C. spectabile* Sw. = *C. reginae* Walt.
    - c. Diphylla group (lateral sepals fused, foliage leaves only two)
        - *C. japonicum* Thunb.
2. *Selenipedilum* Rchb. f. = *Selenipedium* Rchb. f. (leaf vernation convolute, ovaries trilocular, testa of seed crustose)
    - *S. chica* Rchb. f.
3. *Paphiopedilum* Pfitz. (leaf vernation conduplicate, testa thin)
    - a. Genuina group (inflorescences one-flowered, Asiatic)
        - *P. barbatum* (Lindl.) Pfitz.
        - *P. boxallii* (Rchb. f.) Pfitz.
        - *P. concolor* (Batem.) Pfitz.
        - *P. insigne* (Wall. ex Lindl.) Pfitz.
    - b. Caudata group (inflorescences many-flowered)
        - *P. caudatum* (Lindl.) Pfitz. (including *Uropedilum lindenii* Lindl.)
        - *P. laevigatum* (Batem.) Pfitz. = *P. philippinense* (Rchb. f.) Stein *s. amplo*
        - *P. longifolium* (Rchb. f. & Warsz.) Pfitz.

Appendix 3. Classification of the Cypripedioideae (Cypripedilinae) according to Pfitzer (1894) including orthographic changes. Many of the *Paphiopedilum* combinations should be credited to Stein (see Appendix 9).

1. *Selenipedilum* Rchb. f. = *Selenipedium* Rchb. f.
   S. chica Rchb. f.
   S. isabelianum Barb. Rodr.
   S. palmifolium (Lindl.) Rchb. f.

2. *Cypripedilum* L. = *Cypripedium* L.
   A. Eucypripedilum group
   a. Multiflora
   C. californicum A. Gray
   b. Pauciflora
   C. acaule Sw. = *C. acaule* Ait.
   C. calceolus L.
   C. candidum Muhlenb. ex Willd.
   C. cordigerum D. Don
   C. debile Rchb. f.
   C. elegans Rchb. f.
   C. fasciculatum Kell. ex S. Wats.
   C. guttatum Sw.
   C. irapeanum Llave & Lex.
   C. macranthum Sw.
   C. montanum Dougl. ex Lindl.
   C. occidentale S. Wats. = *C. montanum* Dougl. ex Lindl.
   C. parviflorum Salisb.
   C. passerinum Richards.
   C. pubescens Willd.
   C. spectabile Sw. = *C. reginae* Walt.
   C. thunbergii Bl.
   C. ventricosum Sw.
   c. Diphylla group
   C. japonicum Thunb.
   B. Trigonopedilum Franch. group
   C. margaritaceum Franch.
   C. Arietinum Beck group
   C. arietinum R. Br.
   C. plectrochilum Franch.

3. *Paphiopedilum* Pfitz.
   A. Coelopedilum group
   a. Eremantha
   1. Tessellata
   P. argus (Rchb. f.) Pfitz.
   P. barbatum (Lindl.) Pfitz.
   P. bellatulum (Rchb. f.) Pfitz.
   P. boxallii (Rchb. f.) Pfitz.
   P. bullenianum (Rchb. f.) Pfitz.
   P. burbidgei (Rchb. f.) Pfitz.
   P. callosum (Rchb. f.) Pfitz.
   P. charlesworthii (Rolfe) Pfitz.
   P. ciliolare (Rchb. f.) Pfitz.
   P. concolor (Par.) Pfitz. = *P. concolor* (Batem.) Pfitz.
   P. curtisii (Rchb. f.) Pfitz.
   P. dayanum (Rchb. f.) Pfitz.
   P. dilectum (Rchb. f.) Pfitz.
   P. godefroyae (Godefroy) Pfitz.
   P. hookerae (Rchb. f.) Pfitz.
   P. javanicum (Reinw. ex Lindl. & Paxt.) Pfitz
   P. lawrenceanum (Rchb. f.) Pfitz.
   P. mastersianum (Rchb. f.) Pfitz.
   P. nigritum (Rchb. f.) Pfitz.
   P. niveum (Rchb. f.) Pfitz.
   P. pardinum (Rchb. f.) Pfitz.
   P. petri (Rchb. f.) Pfitz.
   P. purpuratum (Lindl.) Pfitz.
   P. superbiens (Rchb. f.) Pfitz.
   P. tonsum (Rchb. f.) Pfitz.
   P. venustum (Wall. ex Sims) Pfitz.
   P. virens (Rchb. f.) Pfitz.
   2. Viridia
   P. druryi (Bedd.) Pfitz.
   P. fairieanum (Lindl.) Pfitz.
   P. hirsutissimum (Lindl.) Pfitz.
   P. insigne (Wall. ex Lindl.) Pfitz.
   P. spicerianum (Rchb. f.) Pfitz.
   P. villosum (Lindl.) Pfitz.
   b. Polyantha
   P. chamberlainianum (O'Brien) Pfitz.
   P. elliottianum (O'Brien) Pfitz.
   P. gardineri (Guill.) Pfitz.
   P. glanduliferum (Bl.) Pfitz.
   P. haynaldianum (Rchb. f.) Pfitz.
   P. lowii (Lindl.) Pfitz.
   P. parishii (Rchb. f.) Pfitz.
   P. philippinense (Rchb. f.) Pfitz.
   P. praestans (Rchb. f.) Pfitz.
   P. roebbelenii (Rchb. f.) Pfitz.
   P. rothschildianum (Rchb. f.) Pfitz.
   P. sanderianum (Rchb. f.) Pfitz.
   P. stonei (Hook. f.) Pfitz.

B. Phragmopedilum group
Paphiopedilum boissierianum (Rchb. f.) Pfitz.
P. caricinum (Lindl. ex Paxt.) Pfitz.
P. caudatum (Lindl.) Pfitz.
P. czerwiakowianum (Rchb. f.) Pfitz.
P. hartwegii (Rchb. f.) Pfitz.
P. hincksianum (Rchb. f.) Pfitz. =
P. klotzscheanum (Rchb. f.) Rolfe
P. lindleyanum (Schomb. ex Lindl.) Pfitz.
P. longifolium (Rchb. f. & Warsz.) Pfitz.
P. reticulatum (Rchb. f.) Pfitz.
P. schlimii (Batem.) Pfitz. =
P. schlimii (Lindl. & Rchb. f.)
P. vittatum (Vell.) Pfitz.
P. warscewiczii (Rchb. f.) Pfitz.

Appendix 4. Classification of the Cypripedioideae (Tribe II, Cypripedieae) according to Rolfe, 1896.

1. *Selenipedium* Rchb. f.
S. chica Rchb. f.
S. isabelianum Barb. Rodr.
S. palmifolium (Lindl.) Rchb. f.

2. *Phragmipedium* Rolfe
P. boissierianum (Rchb. f.) Rolfe
P. caricinum (Lindl. & Paxt.) Rolfe
P. caudatum (Lindl.) Rolfe
P. czerwiakowianum (Rchb. f.) Rolfe
P. klotzscheanum (Rchb. f.) Rolfe
P. lindleyanum (Schomb. ex Lindl.) Rolfe
P. longifolium (Rchb. f. & Warsz.) Pfitz.
P. sargentianum (Rolfe) Rolfe
P. schlimii (Lindl. & Rchb. f.) Rolfe
P. vittatum (Vell.) Rolfe

3. *Cypripedium* L.
C. acaule Ait.
C. arietinum R. Br.
C. calceolus L.
C. californicum A. Gray
C. candidum Muhlenb. ex Willd.
C. cordigerum D. Don.
C. debile Rchb. f.
C. ebracteatum Rolfe
C. elegans Rchb. f.
C. fargesii Franch.
C. fasciculatum Kell. ex S. Wats.
C. fasciolatum Franch.
C. guttatum Sw.
C. henryi Rolfe
C. himalaicum Rolfe
C. irapeanum Llave & Lex.
C. japonicum Thunb.
C. luteum Franch.
C. macranthum Sw.
C. margaritaceum Franch.
C. micranthum Franch.
C. montanum Dougl. ex Lindl.
C. parviflorum Salisb.
C. passerinum Richards.
C. pubescens Willd.
C. reginae Walt.
C. tibeticum King ex Rolfe
C. yunnanense Franch.

4. *Paphiopedium* Pfitzer = *Paphiopedilum* Pfitzer
P. appletonianum (Gower) Rolfe
P. argus (Rchb. f.) Pfitz.
P. barbatum (Lindl.) Pfitz.
P. bellatulum (Rchb. f.) Pfitz.
P. boxallii (Rchb. f.) Pfitz.
P. bullenianum (Rchb. f.) Pfitz.
P. callosum (Rchb. f.) Pfitz.
P. chamberlainianum (O'Brien) Pfitz.
P. charlesworthii (Rolfe) Pfitz.
P. ciliolare (Rchb. f.) Pfitz.
P. concolor (Batem.) Pfitz.
P. curtisii (Rchb. f.) Pfitz.
P. dayanum (Rchb. f.) Pfitz.
P. druryi (Bedd.) Pfitz.
P. exul (Ridley) Rolfe =
P. insigne (Wall. ex Lindl.) Pfitz.
P. javanicum (Reinw. ex Lindl. & Paxt.) Pfitz.
P. lawrenceanum (Rchb. f.) Pfitz.
P. lowii (Lindl.) Pfitz.
P. mastersianum (Rchb. f.) Pfitz.
P. nigritum (Rchb. f.) Pfitz.
P. niveum (Rchb. f.) Pfitz.
P. parishii (Rchb. f.) Pfitz.
P. philippinense (Rchb. f.) Pfitz.
P. praestans (Rchb. f.) Pfitz.
P. purpuratum (Lindl.) Pfitz.
P. rothschildianum (Rchb. f.) Pfitz.
P. sanderianum (Rchb. f.) Pfitz.
P. spicerianum (Rchb. f.) Pfitz.

P. fairieanum (Lindl.) Pfitz.
P. glanduliferum (Bl.) Pfitz.
P. godefroyae (Godefroy) Pfitz.
P. haynaldianum (Rchb. f.) Pfitz.
P. hirsutissimum (Lindl.) Pfitz.
P. hookerae (Rchb. f.) Pfitz.
P. stonei (Hook. f.) Pfitz.
P. superbiens (Rchb. f.)
P. tonsum (Rchb. f.) Pfitz.
P. venustum (Wall. ex Sims) Pfitz.
P. victoria-mariae (Sand. ex Masters) Rolfe = *P. victoria-regina* (Sand.) M. W. Wood
P. villosum (Lindl.) Pfitz.
P. virens (Rchb. f.) Pfitz.

Appendix 5. Classification of *Paphiopedilum* Pfitz. according to Hallier (1897). Many combinations formerly attributed to Pfitzer should be credited to Stein. The outline below is taken as it appears in Hallier.

A. Coelopedilum Pfitz. (ovaries unilocular)
a. Aphanoneura
I. Brachypetalum
P. bellatulum (Rchb.f.) Pfitz.;
P. concolor (Par.) Pfitz. = *P. concolor* (Batem.) Pfitz.
P. godefroyae (Godefroy) Pfitz.
P. niveum (Rchb. f.) Pfitz.
b. Chromatoneura
1. Tessellata
II. Sigmopetalum
*Chloroneura
P. amabile Hallier f.
P. bullenianum (Rchb. f.) Pfitz.
P. hookerae (Rchb. f.) Pfitz.
P. javanicum (Reinw. ex Lindl. & Paxt.) Pfitz.
P. mastersianum (Rchb. f.) Pfitz.
P. pardinum (Rchb. f.) Pfitz. = *P. venustum* (Wall. ex Sims) Pfitz.
P. venustum (Wall. ex Sims) Pfitz.
P. virens (Rchb. f.) Pfitz.
** Erythoneura
P. barbatum (Lindl.) Pfitz.
P. callosum (Rchb. f.) Pfitz.
P. lawrenceanum (Rchb. f.) Pfitz.
III. Clinopetalum
P. argus (Rchb. f.) Pfitz.
P. ciliolare (Rchb. f.) Pfitz.
P. superbiens (Rchb. f.) Pfitz.
IV. Drepanopetalum
P. burbidgei (Rchb. f.) Pfitz.
P. curtisii (Rchb. f.) Pfitz.
P. dayanum (Rchb. f.) Pfitz.
P. nigritum (Rchb. f.) Pfitz.
P. petri (Rchb. f.) Pfitz.
P. purpuratum (Lindl.) Pfitz.
2. Viridia
a. Eremantha Pfitz.
V. Thiopetalum
P. druryi (Bedd.) Pfitz.
VI. Ceratopedilum
P. fairieanum (Lindl.) Pfitz.
VII. Cymatopetalum
P. spicerianum (Rchb. f.) Pfitz.
VIII. Stictopetalum
P. hirsutissimum (Lindl.) Pfitz.
IX. Neuropetalum
P. boxallii (Rchb. f.) Pfitz.

P. charlesworthii (Rolfe) Pfitz.
P. insigne (Wall. ex Lindl.) Pfitz.
P. villosum (Lindl.) Pfitz.

b. Polyantha Pfitz.
X. Pardolopetalum
P. haynaldianum (Rchb. f.) Pfitz.
P. lowii (Lindl.) Pfitz.
XI. Streptopetalum
P. glanduliferum (Bl.) Pfitz.
P. parishii (Rchb. f.) Pfitz.
P. philippinense (Rchb. f.) Pfitz.
P. praestans (Rchb. f.) Pfitz.
P. roebbelenii (Rchb. f.) Pfitz.
XII. Mastigopetalum
P. elliottianum (O'Brien) Pfitz.
P. rothschildianum (Rchb. f.) Pfitz.
P. sanderianum (Rchb. f.) Pfitz.
P. stonei (Hook. f.) Pfitz.
XIII. Cochlopetalum
P. chamberlainianum (O'Brien) Pfitz.
B. Phragmopedilum Pfitz. (= *Phragmipedium* Rolfe, the genus)
XIV. Himantopetalum
Paphiopedilum boissierianum (Rchb. f.) Pfitz.
P. caricinum (Lindl. & Paxt.) Pfitz.
P. caudatum (Lindl.) Pfitz.
P. czerwiakowianum (Rchb. f.) Pfitz.
P. klotzscheanum(Rchb. f.) Rolfe
P. lindleyanum (Schomb. ex Lindl.) Pfitz.
P. longifolium (Rchb. f. ex Warsz.) Pfitz.
P. reticulatum (Rchb. f.) Pfitz.
P. sargentianum (Sand.) Hallier
P. vittatum (Vell.) Pfitz.
XV. Micropetalum Hallier
P. schlimii (Rchb. f.) Pfitz.

Appendix 6. Classification of the Cypripedioideae according to Kraenzlin (1901). The indicated groups and subgroups are non-taxonomic categories.

I. Section *Calceolaria*
1. Calceolus group
A. Scapes one- or two-flowered
C. calceolus L.
C. candidum Muhlenb. ex Willd.
C. cordigerum D. Don
C. fasciolatum Franch.
C. henryi Franch. = *C. henryi* Rolfe ?
C. montanum Dougl. ex Lindl.
C. parviflorum Salisb.
C. pubescens Willd.
C. thunbergii Bl.
C. yunnanense Franch.
B. Scapes many-flowered
C. californicum A. Gray
C. fasciculatum Kell. ex S. Wats.
C. irapeanum Llave & Lex.
2. Macrantha group
C. corrugatum Franch.
C. humile Salisb. = *C. acaule* Ait.
C. macranthum Sw.
3. Bifolia group
A. Ebracteata subgroup
C. ebracteatum Rolfe
C. margaritaceum Franch.
C. micranthum Franch.
B. Bracteosa subgroup
C. debile Rchb. f.
C. elegans Rchb. f.
C. guttatum Sw.
C. japonicum Thunb.

- 4. Obtusiflora group
    - *C. luteum* Franch.
    - *C. passerinum* Richards.
    - *C. spectabile* Salisb. = *C. reginae* Walt.
- 5. Arietinia group
    - *C. arietinum* R. Br.

- II. Section *Selenipedia*
    - *C. chica* Rchb. f.
    - *C. isabelianum* (Barb. Rodr.) Pucci
    - *C. palmifolium* Lindl.
- III. Section *Lorifolia*
    - *C. lindleyanum* Schomb. ex Lindl.
    - *C. longifolium* Rchb. f. & Warsz.
    - *C. sargentianum* Rolfe
    - *C. schlimii* Batem. = *C. schlimii* Lind. & Rchb. f.
    - *C. vittatum* Vell.
- IV. Section *Caudata*
    - *C. boissierianum* Rchb. f. *(Phrag.)*
    - *C. caricinum* Lindl. & Paxt. *(Phrag.)*
    - *C. caudatum* Lindl. *(Phrag.)*
    - *C. czerwiakowianum* Rchb. f. *(Phrag.)*
    - *C. parishii* Rchb. f. *(Paph.)*
    - *C. philippinense* Rchb. f. *(Paph.)*
    - *C. roebbelinii* Rchb. f. *(Paph.)*
    - *C. rothschildianum* Rchb. f. *(Paph.)*
    - *C. sanderianum* Rchb. f. *(Paph.)*
    - *C. stonei* Low. = *C. stonei* Hook. f.? *(Paph.)*
- V. Section *Barbata*
    - *C. argus* Rchb. f.
    - *C. barbatum* Lindl.
    - *C. callosum* Rchb. f.
    - *C. ciliolare* Rchb. f.
    - *C. curtisii* Rchb. f.
    - *C. dayanum* Rchb. f.
    - *C. dilectum* Rchb. f.
    - *C. elliottianum* O'Brien
    - *C. glanduliferum* Bl.
    - *C. haynaldianum* Rchb. f.
    - *C. hookerae* Rchb. f.
    - *C. javanicum* Reinw. ex Lindl. & Paxt
    - *C. lawrenceanum* Rchb. f.
    - *C. lowii* Lindl.
    - *C. mastersianum* Rchb. f.
    - *C. nigritum* Rchb. f.
    - *C. purpuratum* Lindl.
    - *C. superbiens* Rchb. f.
    - *C. tonsum* Rchb. f.
    - *C. virens* Rchb. f.
    - *C. wolterianum* Krzl.
- VI. Section *Concoloria*
    - *C. bellatulum* Rchb. f.
    - *C. concolor* Batem.
    - *C. godefroy* Godefroy
    - *C. niveum* Rchb. f.
- VII. Section *Insignia*
    - *C. chamberlainianum* O'Brien
    - *C. charlesworthii* Rolfe
    - *C. druryi* Bedd.
    - *C. fairieanum* Lindl.
    - *C. hirsutissimum* Lindl.
    - *C. insigne* Wall. ex Lindl.
    - *C. spicerianum* Rchb. f.
    - *C. venustum* Wall. ex Sims
    - *C. villosum* Lindl.

Appendix 7. Classification of the Cypripedioideae (Tribe Cypripedilinae) according to Pfitzer (1903).

- I. *Selenipedilum* Rchb. f. *emend.* Pfitz.
    - *S. chica* Rchb. f.
    - *S. isabelianum* Barb. Rodr.
    - *S. palmifolium* (Lindl.) Rchb. f.
- II. *Cypripedilum* L. = *Cypripedium* L.
    - A. Series *Arcuinerva* Pfitz.
        - 1. Section *Eucypripedilum* Pfitz.
            - a. Subsection *Obtusipetala* Pfitz.
                - *C. californicum* A. Gray
                - *C. guttatum* Sw.
                - *C. irapeanum* Llave & Lex.
                - *C. luteum* Franch.
                - *C. passerinum* Richards.
                - *C. reginae* Walt.

b. Subsection *Acutipetala* Pfitz.
C. acaule Ait.
C. calceolus L.
C. candidum Muhlenb. ex Willd.
C. cordigerum D. Don
C. corrugatum Franch.
C. fasciolatum Franch.
C. henryi Rolfe
C. himalaicum Rolfe
C. macranthum Sw.
C. montanum Dougl. ex Lindl.
C. parviflorum Salisb.
C. pubescens Willd.
C. thunbergii Bl.
C. yunnanense Franch.
2. Section *Enantiopedilum* Pfitz.
C. ebracteatum Rolfe
C. fasciculatum Kell. ex S. Wats.
C. micranthum Franch.
3. Section *Trigonopedilum* Franch.
C. margaritaceum Franch.
4. Section *Criosanthes* Raf.
C. arietinum R. Br.
B. Series *Retinervia* Pfitz.
C. debile Rchb. f.
C. elegans Rchb. f.
C. Series *Flabellinervia* Pfitz.
C. japonicum Thunb.
III. *Phragmopedilum* (Pfitz.) Rolfe - *Phragmipedium* Rolfe
A. Section *Micropetalum* (Hall.) Pfitz.
P. schlimii (Lindl. & Rchb. f.) Rolfe
B. Section *Platypetalum* Pfitz.
P. lindleyanum (Schomb. ex Lindl.) Rolfe
P. sargentianum (Rolfe) Rolfe
C. Section *Himantopedilum* Pfitz.
P. caricinum (Lindl. & Paxt.) Rolfe
P. klotzscheanum (Rchb. f.) Rolfe
D. Section *Ceratopedilum* Pfitz.
P. boissierianum (Rchb. f.) Rolfe
P. czerwiakowianum (Rchb. f.) Rolfe
P. hartwegii (Rchb. f.) Pfitz.
P. longifolium (Rchb. f. & Warsz.) Rolfe
P. vittatum (Vell.) Rolfe
E. Section *Desmopedilum* Pfitz.
P. caudatum (Lindl.) Rolfe
IV. *Paphiopedilum* Pfitz.
A. Subgenus *Brachypetalum* (Hall.) Pfitzer
P. bellatulum (Rchb. f.) Pfitz.
P. concolor (Batem.) Pfitz.
P. godefroyae (Godefroy) Pfitz.
P. niveum (Rchb. f.) Pfitz.
B. Subgenus *Anotopedilum* Pfitz.
1. Section *Gonatopedilum* Pfitz.
P. rothschildianum (Rchb. f.) Pfitz.
2. Section *Coryopedilum* Pfitz.
P. glanduliferum (Bl.) Pfitz.
P. philippinense (Rchb. f.) Pfitz.
P. praestans (Rchb. f.) Pfitz.
P. roebbelenii (Rchb. f.) Pfitz.
P. sanderianum (Rchb. f.) Pfitz.
3. Section *Prenipedilum* Pfitz.
P. stonei (Hook. f.) Pfitz.
C. Subgenus *Otopedilum* Pfitz.
1. Section *Mystropetalum* Pfitz.
P. parishii (Rchb. f.) Pfitz.
2. Section *Pardalopetalum* (Hall.) Pfitz.
P. haynaldianum (Rchb.f.) Pfitz.
P. lowii (Lindl.) Pfitz.
3. Section *Cochlopetalum* (Hall.) Pfitz.
P. chamberlainianum (O'Brien) Pfitz.
P. glaucophyllum J. J. Sm.
P. victoria-mariae (Sand. ex Masters) Rolfe = *P. victoria-regina* (Sand.) M. W. Wood
4. Section *Stictopetalum* (Hall.) Pfitz.
P. hirsutissimum (Lindl.) Pfitz.
5. Section *Neuropetalum* (Hall.) Pfitz.
P. charlesworthii (Rolfe) Pfitz.
P. dilectum (Rchb. f.) Pfitz.
P. exul (O'Brien) Pfitz. = *P. exul* (Ridley) Pfitz.?
P. insigne (Wall. ex Lindl.) Pfitz.
P. villosum (Lindl.) Pfitz.
6. Section *Thiopetalum* (Hall.) Pfitz.
P. druryi (Bedd.) Stein
7. Section *Cymatopetalum* (Hall.) Pfitz.
P. spicerianum (Rchb. f.) Pfitz.
8. Section *Ceratopetalum* (Hall.) Pfitz.
P. fairieanum (Lindl.) Pfitz.

- 9. Section *Spathopetalum* Pfitz.
  - *P. amabile* Hall.
  - *P. appletonianum* (Gower) Rolfe
  - *P. bullenianum* (Rchb. f.) Pfitz.
  - *P. hookerae* (Rchb. f.) Pfitz.
  - *P. venustum* (Wall. ex Sims) Pfitz.
  - *P. volonteanum* (Sand.) Pfitz.
  - *P. wolterianum* (Krzl.) Pfitz.
- 10. Section *Blepharopetalum* Pfitz.
  - *P. burbidgei* (Rchb. f.) Pfitz.
  - *P. dayanum* (Rchb. f.) Pfitz.
  - *P. javanicum* (Reinw. ex Lindl. & Paxt.) Pfitz.
  - P. *mastersianum* (Rchb. f.) Pfitz.
  - *P. purpuratum* (Lindl.) Pfitz.
  - *P. tonsum* (Rchb. f.) Pfitz.
  - *P. virens* (Rchb. f.) Pfitz.
- 11. Section *Phacopetalum* Pfitz.
  - *P. argus* (Rchb. f.) Pfitz.
  - *P. barbatum* (Lindl.) Pfitz.
  - *P. callosum* (Rchb. f.) Pfitz.
  - *P. ciliolare* (Rchb. f.) Pfitz.
  - *P. curtisii* (Rchb. f.) Pfitz.
  - *P. lawrenceanum* (Rchb. f.) Pfitz.
  - *P. superbiens* (Rchb. f.) Pfitz.

Appendix 8. Classification of the Cypripedioideae according to Brieger (1971).

- I. Tribe Selenipedieae Brieger
  - A. Subtribe Selenipediinae Brieger
    - 1. *Selenipedium* Rchb. f.
      - *S. chica* Rchb. f.
      - *S. isabelianum* Barb. Rodr.
      - *S. palmifolium* (Lindl.) Rchb. f.
      - *S. steyermarkii* Foldats
- II. Tribe Phragmipedieae Brieger
  - A. Subtribe Phragmipediinae Brieger
    - 1. *Phragmipedium* Rolfe
      - a. Subgenus *Micropetalum* (Hall.) Brieg.
        - *P. schlimii* (Lind. & Rchb. f.) Rolfe
      - b. Subgenus *Phragmipedium*
        - *P. boissierianum* (Rchb. f.) Rolfe
        - *P. caricinum* (Lindl. & Paxt.) Rolfe
        - *P. caudatum* (Lindl.) Rolfe
        - *P. czerwiakowianum* (Rchb. f.) Rolfe
        - *P. hartwegii* (Rchb. f.) Pfitz.
        - *P. klotzscheanum* (Rchb. f.) Rolfe
        - *P. longifolium* (Rchb. f.) & Warsz.) Rolfe
        - *P. vittatum* (Vell.) Rolfe
      - c. Subgenus *Platypetalum* (Pfitz.) Brieg.
        - *P. lindleyanum* (Schomb. ex Lindl.) Rolfe
        - *P. sargentianum* (Rolfe) Rolfe
- III. Tribe Paphiopedileae Brieger
  - A. Subtribe Paphiopedilinae Brieger
    - 1. *Paphiopedilum* Pfitz.
      - a. Subgenus *Polyantha* Pfitz.
        - 1. Section *Mastigopetalum* (Hall.) Brieger
          - *P. philippinense* (Rchb. f.) Pfitz.
          - *P. praestans* (Rchb. f.) Pfitz.
          - *P. roebbelinii* (Rchb. f.) Pfitz.
          - *P. rothschildianum* (Rchb. f.) Pfitz.
          - *P. stonei* (Hook. f.) Pfitz.
        - 2. Section *Streptopetalum* (Hall.) Brieger
          - *P. glanduliferum* (Bl.) Pfitz.
          - *P. sanderianum* (Rchb. f.) Pfitz.
          - *P. wilhelminiae* L. O. Wms.
        - 3. Section *Polyantha* Pfitz. (= Section *Pardalopetalum* (Hall.) Pfitz.)
          - *P. dianthum* Tang & Wang
          - *P. haynaldianum* (Rchb. f.) Pfitz.
          - *P. lowii* (Lindl.) Pfitz.
          - *P. parishii* (Rchb. f.) Pfitz.
        - 4. Section *Cochlopetalum* (Hall.) Pfitz.
          - *P. chamberlainianum* (O'Brien) Pfitz.
          - *P. glaucophyllum* J. J. Sm.
          - *P. victoria-mariae* (Sand. Ex Masters) Rolfe =
            P. victoria-regina (Sand.) M. W. Wood
      - b. Subgenus *Paphiopedilum*
        - 1. Section *Stictopetalum* (Hall.) Pfitz.
          - *P. affine* DeWild.
          - *P. barbigerum* Tang & Wang
          - *P. charlesworthii* (Rolfe) Pfitz.
          - *P. gratrixianum* Guill.
          - *P. hirsutissimum* (Lindl.) Pfitz.
          - *P. insigne* (Wall. ex Lindl.) Pfitz.

P. chiwuanum Tang & Wang
P. druryi (Benth.) Pfitz. = *P. druryi* (Bedd.) Stein
P. esquirolei Schltr.
P. exul (Ridley) Pfitz.
P. micranthum Tang & Wang
P. spicerianum (Rchb. f.) Pfitz.
P. villosum (Lindl.) Pfitz.

c. Subgenus *Barbata* (Krzl.) Brieger
1. Section *Sigmatopetalum* Hall.
P. amabile Hall.
P. appletonianum (Gower) Rolfe
P. bullenianum (Rchb. f.) Pfitz.
P. hookerae (Rchb. f.) Pfitz.
P. javanicum (Reinw. ex Lindl. & Paxt.) Pfitz.
P. linii Schoser
P. mastersianum (Rchb. f.) Pfitz.
P. papuanum (Ridley) L. O. Wms.
P. tonsum (Rchb. f.) Pfitz.
P. venustum (Wall. ex Sims) Pfitz.
P. virens (Rchb. f.) Pfitz.
P. volonteanum (Sand.) Pfitz.
P. wentworthianum Schoser & Fowlie
P. wolterianum (Krzl.) Pfitz.
P. zieckianum Schoser

2. Section *Blepharopetalum* Pfitz.
P. burbidgei (Rchb. f.) Pfitz.
P. curtisii (Rchb. f.) Pfitz.
P. dayanum (Rchb. f.) Pfitz.
P. purpuratum (Lindl.) Pfitz.
P. sukhakulii Schoser & Sengh.
P. violascens Schltr.
P. wardii Summerhayes

3. Section *Barbata* Krzl. (= *Phacopetalum* Pfitz.)
P. acmodontum Schoser ex M. W. Wood
P. argus (Rchb. f.) Pfitz.
P. barbatum (Lindl.) Pfitz.
P. callosum (Rchb. f.) Pfitz.
P. ciliolare (Rchb. f.) Pfitz.
P. fairieanum (Lindl.) Pfitz.
P. hennisianum (Shoser ex M. W. Wood) Fowlie
P. lawrenceanum (Rchb. f.) Pfitz.
P. nigritum (Rchb. f.) Pfitz.
P. randsii Schoser
P. superbiens (Rchb. f.) Pfitz.

d. Subgenus *Brachypetalum* (Hall.) Pfitz.
P. bellatulum (Rchb. f.) Pfitz.
P. concolor (Batem.) Pfitz.
P. delenatii Guill.
P. godefroyae (Godefroy) Pfitz.
P. niveum (Rchb. f.) Pfitz.

IV. Tribe Cypripedieae Brieger
A. Subtribe Cypripediinae Brieger
1. *Cypripedium* L.
a. Subgenus *Cypripedium*
C. arietinum R. Br.
C. calceolus group
C. calceolus L.
C. candidum Muhlenb. ex Willd.
C. cordigerum D. Don
C. henryi (Rolfe) (including *C. chinense* Franch.)
C. microsaccus Krzl.
C. montanum Dougl. ex Lindl.
C. pubescens Willd.
C. californicum A. Gray
C. irapeanum Llave & Lex.
C. luteum Franch.
C. macranthum group
C. corrugatum Franch.
C. fasciolatum Franch. (including *C. franchetii* Rolfe
C. himalaicum Rolfe
C. macranthum Sw.
C. manchuricum Stapf
C. tibeticum King ex Hemsl.
C. yunnanense Franch.
C. passerinum Richards.
C. reginae Walt.

b. Subgenus *Guttata* Brieger
C. guttatum Sw.
C. yatabeanum Makino

c. Subgenus *Acaulia* Brieger
C. acaule Ait.
C. nutans Schltr.
C. wardii Rolfe

d. Subgenus *Ebracteata* Franch.
C. bardophianum W.W.Sm. & Farrer
C. ebracteatum Rolfe
C. margaritaceum Franch.
C. micranthum Franch.

e. Subgenus *Fasciculata* Brieger
C. fasciculatum Kell. ex S. Wats.

f. Subgenus *Flabellinervia* Pfitz.

- *C. japonicum* Thunb.
- g. Subgenus *Retinervia* Pfitz.
  - *C. debile* Rchb. f.
  - *C. elegans* Rchb. f.
  - *C. parvum* Brieger

Appendix 9. Binomials which are used throughout this work. Species names of the conduplicate-leaved genera are distributed according to the classification proposed in Chapter 4.

1. *Criosanthes* Raf.
   - *C. arietina* (R. Br.) House
   - *C. plectrochila* Franch.
2. *Cypripedium* L.
   - *C. acaule* Ait.
   - *C. bardolphianum* W. W. Sm. & Farrer
   - *C. calceolus* L. This and the following form a circumboreal complex.
     - *C. candidum* Muhlenb. ex Willd.
     - *C. cordigerum* D. Don
     - *C. henryi* Rolfe
     - *C. microsaccus* Krzl.
     - *C. montanum* Dougl. ex Lindl.
     - *C. parviflorum* Salisb.
     - *C. planipetalum* (Fern.) Morris & Eames
     - *C. pubescens* Willd.
   - *C. californicum* A. Gray
   - *C. candidum* Muhlenb. ex Willd. (See also *C. calceolus* L.)
   - *C. cathayanum* Chien. Perhaps this is conspecific with *C. japonicum* Thunb.
   - *C. cordigerum* D. Don (See also *C. calceolus* L.)
   - *C. corrugatum* Franch. (See also *C. macranthum* Sw.)
   - *C. debile* Rchb. f.
   - *C. ebracteatum* Rolfe
   - *C. elegans* Rchb. f.
   - *C. fargesii* Franch. Apparently related to if not conspecific with *C. margaritaceum* Franch.
   - *C. fasciculatum* Kell. ex S. Wats.
   - *C. fasciolatum* Franch. (including *C. franchetii* Rolfe sensu Brieger)
   - *C. guttatum* Sw. (including *C. yatabeanum* Makino)
   - *C. henryi* Rolfe (= *C. chinense* Franch.? See also *C. calceolus* L.)
   - *C. himalaicum* Rolfe (See also *C. macranthum* Sw.)
   - *C. irapeanum* Llave & Lex. (including *C. molle* Lindl.)
   - *C. japonicum* Thunb. This species and the following may be conspecific.
     - *C. cathayanum* Chien
     - *C. formosanum* Hayata
   - *C. luteum* Franch.
   - *C. macranthum* Sw. This and the following form a complex.
     - *C. corrugatum* Franch.
     - *C. fasciolatum* Franch.
     - *C. himalaicum* Rolfe
     - *C. speciosum* Rolfe
     - *C. thunbergii* Bl.
     - *C. tibeticum* King ex Rolfe
     - *C. ventricosum* Sw.
     - *C. wilsoni* Rolfe
     - *C. yunnanense* Franch.
   - *C. manchuricum* Stapf
   - *C. margaritaceum* Franch.
   - *C. micranthum* Franch.
   - *C. microsaccus* Krzl. (See also *C. calceolus* L.)
   - *C. montanum* Dougl. ex Lindl. (See also *C. calceolus* L.)
   - *C. nutans* Schltr. (This is close to *C. acaule* according to Brieger)
   - *C. parviflorum* Salisb. (See also *C. calceolus* L.)

- *C. parvum* Brieger
- *C. passerinum* Richards.
- *C. planipetalum* (Fern.) Morris & Eames (See also *C. calceolus* L.)
- *C. pubescens* Willd. (See also *C. calceolus* L.)
- *C. reginae* Walt.
- *C. speciosum* Rolfe (See also *C. macranthum* Sw.)
- *C. thunbergii* Bl. (See *C. macranthum* Sw.)
- *C. tibeticum* King ex Hemsl. (See also *C. macranthum* Sw.)
- *C. ventricosum* Sw. (See also *C. macranthum* Sw.)
- *C. wardii* Rolfe (related to *C. acaule* according to Brieger, 1971)
- *C. wilsoni* Rolfe (See also *C. macranthum* Sw.)
- *C. yunnanense* Franch. (See also *C. macranthum* Sw.)

Obscure concepts
- *C. amesianum* Schltr.
- *C. calcicola* Schltr.
- *C. compactum* Schltr.
- *C. farreri* W. W. Smith
- C. *lanuginosum* Schltr.
- *C. palangshanense* Tang & Wang
- *C. pulchrum* Ames & Schltr.
- *C. smithii* Schltr.
- *C. turgidum* Sesse & Moc.
- *C. vernayi* F. K. Ward

3. *Selenipedium* Rchb. f.
   - *S. aequinoctiale* Garay
   - *S. chica* Rchb. f.
   - *S. isabelianum* Barb. Rodr.
   - *S. palmifolium* (Lindl.) Rchb. f.
   - *S. steyermarkii* Foldats
   - *S. vanillocarpum* Barb. Rodr.
4. *Phragmipedium* Rolfe
   - Section *Phragmipedium*
     - *P. caudatum* (Lindl.) Rolfe
     - *P. lindenii* (Lindl.) Dressler & N. Williams
     - *P. wallisii* (Rchb. f.) Garay. This appears to represent allogamous populations of *P. lindenii.*
     - *P. warscewiczianum* (Rchb. f.) Garay
   - Section *Lorifolia* (Krzl.) Garay
     - *P. boissierianum* (Rchb. f.) Rolfe. The following are included with this concept.
       - *P. czerwiakowianum* (Rchb. f.) Rolfe
       - *P. reticulatum* (Rchb. f.) Garay
     - *P. caricinum* (Lindl. & Paxt.) Rolfe
     - *P. ecuadorense* Garay
     - *P. kaieteurum* (N.E. Br.) Garay
     - *P. klotzschianum* (Rchb. f.) Rolfe
     - *P. lindleyanum* (Schomb. ex Lindl.) Rolfe
     - *P. longifolium* (Rchb. f. & Warsz.) Rolfe. The following are here regarded as synonymous.
       - *P. dariense* (Rchb. f.) Garay
       - *P. gracile* Hort.
       - *P. hartwegii* (Rchb. f.) Pfitz.
       - *P. hincksianum* (Rchb. f.) Garay
       - *P. roezlii* (Rchb. f.) Garay
     - *P. pearcei* (Rchb. f.) Rauh & Senghas
     - *P. sargentianum* (Rolfe) Rolfe
     - *P. vittatum* (Vell.) Rolfe
   - Section *Micropetalum* (Hall.) Garay
     - *P. besseae* Dodson & Kuhn
     - *P. schlimii* (Lind. & Rchb. f.) Rolfe
5. *Paphiopedilum* Pfitz.
   - Subgenus *Paphiopedilum*
     - Section *Paphiopedilum*
       - *P. charlesworthii* (Rolfe) Pfitz.
       - *P. chiwuanum* Tang & Wang
       - *P. druryi* (Bedd.) Stein
       - *P. esquirolei* Schltr. Possibly conspecific with *P. hirsutissimum.*
       - *P. exul* (Ridley ex O'Brien) Rolfe
       - *P. fairieanum* (Lindl.) Stein

  - *P. gratrixianum* Guill.
  - *P. hirsutissimum* (Lindl.) Stein
  - *P. insigne* (Wall. ex Lindl.) Pfitz.
  - *P. micranthum* Tang & Wang
  - *P. spicerianum* (Rchb. f.) Pfitz.
  - *P. villosum* (Lindl.) Stein (including *P. boxallii* (Rchb. f.) Pfitz.
- Section *Coryopedilum* Pfitz. *(s. amplo)*
  - *P. elliottianum* (O'Brien) Stein
  - *P. glanduliferum* (Bl.) Stein. This and the following may be conspecific.
    - *P. bodegomii* Hort.
    - *P. gardineri* (Guill.) Pfitz.
    - *P. praestans* (Rchb. f.) Stein
    - *P. wilhelminiae* L. O. Wms.
  - *P. laevigatum* (Batem.) Pfitz.
  - *P. philippinense* (Rchb. f.) Stein. This may be conspecific with the following.
    - *P. laevigatum* (Batem.) Pfitz.
    - *P. roebbelenii* (Rchb. f.) Stein
  - *P. praestans* (Rchb. f.) Pfitz. (See also *P. glanduliferum* (Bl.) Pfitz.
  - *P. randsii* Fowlie
  - *P. roebbelenii* (Rchb. f.) Stein
  - *P. rothschildianum* (Rchb. f.) Stein. Possibly this is conspecific with *P. elliottianum* (O'Brien) Stein.
  - *P. sanderianum* (Rchb. f.) Stein
  - *P. stonei* (Hook. f.) Stein
- Section *Cochlopetalum* (Hall.) Garay
  - *P. victoria-regina* (Sand.) M. W. Wood, including the following subspecies
    - subsp. *chamberlainianum* (Sand.) M. W. Wood
    - subsp. *glaucophyllum* (J. J. Smith) M. W. Wood
    - subsp. *liemianum* (J. A. Fowlie) M. W. Wood
    - subsp. *primulinum* (M. W. Wood & P. Taylor) M. W. Wood
    - subsp. *victoria-regina*
- Section *Pardalopetalum* (Hall.) Pfitz.
  - *P. haynaldianum* (Rchb. f.) Stein
  - *P. lowii* (Lindl.) Stein
  - *P. parishii* (Rchb. f.) Stein. *P. dianthum* Wang & Tang *sensu hortulanorum* may be conspecific.
- Section *Barbata* (Krzl.) Atwood
  - *P. acmodontum* Schoser ex M. W. Wood
  - *P. amabile* Hall. (See also *P. bullenianum* (Rchb. f.) Pfitz.)
  - *P. appletonianum* (Gower) Rolfe. The following may be varieties.
    - *P. johorensis* Fowlie & Yap
    - *P. robinsonii* (Ridley) Ridley
    - *P. wolterianum* (Krzl.) Pfitz.
  - *P. argus* (Rchb. f.) Stein
  - *P. barbatum* (Lindl.) Pfitz. This species apparently forms a cline with *P. callosum*, and the various isolated populations may eventually be found to be best treated as subspecific taxa.
  - *P. bougainvilleanum* Fowlie ex Schoser. This is perhaps only as island population of *P. violascens* Schltr.
  - *P. bullenianum* (Rchb. f.) Pfitz. The following names may eventually be relegated to subspecific categories.
    - *P. amabile* Hall.
    - *P. celebesense* Fowlie & Birk
    - *P. linii* Schoser
    - *P. callosum* (Rchb. f.) Stein (See also *P. barbatum* (Lindl.) Pfitz.)
    - *P. celebesense* Fowlie & Birk. (See also *P. bullenianum* (Rchb. f.) Pfitz.)
    - *P. ciliolare* (Rchb. f.) Stein
    - *P. curtisii* (Rchb. f.) Stein
    - *P. dayanum* (Rchb. f.) Stein
    - *P. fowliei* Birk
    - *P. hennisianum* (Schoser ex M. W. Wood) Fowlie
    - *P. hookerae* (Rchb. f.) Stein. This may include *P. volonteanum* (Sand.) Stein.
    - *P. javanicum* (Reinw. ex Lindl. & Paxt.) Stein
    - *P. lawrenceanum* (Rchb. f.) Stein

- *P. linii* Schoser (See note under *P. bullenianum* (Rchb. f.) Pfitz.)
- *P. mastersianum* (Rchb. f.) Stein. This may include *P. zieckianum* Schoser.
- *P. nigritum* (Rchb. f.) Pfitz. This obscure concept may represent a hybrid with *P. lawrenceanum* as one parent.
- *P. papuanum* (Ridley) L. O. Wms. This is perhaps conspecific with *P. violascens* Schltr.
- *P. purpurascens* Fowlie
- *P. purpuratum* (Lindl.) Stein
- *P. sukhakulii* Senghas & Schoser
- *P. superbiens* (Rchb. f.) Stein. This may be conspecific with *P. curtisii* (Rchb. f.) Stein
- *P. tonsum* (Rchb. f.) Stein
- *P. urbanianum* Hort.
- *P. venustum* (Wall. ex Sims) Pfitz. (including *P. pardinum* (Rchb. f.) Pfitz.)
- *P. violascens* Schltr. This may form a complex with *P. wentworthianum* Schoser & Fowlie
- *P. virens* (Rchb. f.) Pfitz.
- *P. volonteanum* (Sand.) Stein. This may be conspecific with *P. hookerae* (Rchb. f.) Stein.
- *P. wardii* Summerhayes
- *P. wentworthianum* Schoser & Fowlie. (See note under *P. violascens.)*
- *P. ziechianum* Schoser. Perhaps conspecific with *P. mastersianum* (Rchb. f.) Pfitz.

Subgenus *Brachypetalum* (Hall.) Pfitz.
- *P. bellatulum* (Rchb. f.) Stein
- *P. concolor* (Batem.) Pfitz.
- *P. delenatii* Guill.
- *P. godefroyae* (Godefroy) Stein
- *P. niveum* (Rchb. f.) Stein

Obscure concepts
- *P. affine* DeWild.
- *P. barbigerum* Tang & Wang
- *P. burbidgei* (Rchb. f.) Pfitz.
- *P. dilectum* (Rchb. f.) Pfitz. Apparently this is intermediate between *P. hirsutissimum* and *P. villosum* and may be a natural hybrid.

Appendix 10. Specimens examined. Voucher specimens are deposited at the Marie Selby Botanical Gardens unless otherwise indicated. Presumed origins (cultivated material) are indicated by asterisks (*). Many photographs yielding information not preserved in herbarium sheets were also examined but are not here indicated *(Cypripedium fasciculatum*, *C. japonicum*, *C. macranthum*, *C. montanum*, *C. passerinum*, and *Paphiopedilum rothschildeanum).* Collection numbers are my own unless otherwise indicated.

Species	Collection number	Origin
Cypripedium acaule	*77213*	Vermont
C. arietinum	*77208*	Michigan
C. californicum	*Messner s.n. (= Atwood 814)*	California
C. candidum	*77203*	Michigan
C. guttatum	*Sparado s.n. (Atwood 77715)*	Alaska
C. irapeanum	*Breedlove 6462* (FSU), *Stevens, Donoghue & Scott 2307*(MSU)	Mexico
C. parviflorum	*77202*	Michigan
C. pubescens	*77207*	Michigan
C. reginae	*77219*	Vermont
C. formosanum	*Yanazaki, Namba & Tani 732* (FSU)	Taiwan
Selenipedium chica	*77182*	Panama
Phragmipedium boissierianum	*815* (F. Stermitz collection)	Peru
P. caricinum	*7619, 7620, 77189, 77900*	*Bolivia

P. caudatum	*7616*	*Peru
P. lindleyanum	(Live specimen in Selby collection)	*Venezuela
P. longifolium		
entity *longifolium*	*Williams N-1, N-11, N-15* *Atwood 77173-3, 77173-4*	Panama
entity *gracile*	*77177-1, 77177-3, 77177-4* *77177-7, 781-1*	Panama
"hartwegii"	*7623-1, 7623-3*	Ecuador
P. pearcei	*7622, 7621* (from Selby collection)	Ecuador
P. schlimii	*747*	*Colombia
P. wallisii	*7317*	*Ecuador
P. warscewiczianum	*782*	Panama
Paphiopedilum acmodontum	*741-4, 741-3, 741-5*	*Philippines
P. appletonianum	*7325, 7413, 78101, 78102*	*Thailand
P. argus	*732-0, 732-1, 732-2, 732-3*	*Philippines
P. barbatum	*761*	*Malaya
P. bellatulum	*7315*	*Thailand
P. bullenianum	*77196, 763*	*Borneo
P. callosum	*751-1, 754-4, 814*	*Thailand
P. ciliolare	*764, 765-1, 765-2*	*Philippines
P. concolor	*759, 7311, 7614*	*Thailand
P. curtisii	*7518*	*Sumatra
P. delenatii	*7510*	*Vietnam
P. exul	*7612*	*Malaya
P. fairieanum	*7412*	*India
P. godefroyae	*7314*	*Thailand
P. haynaldianum	*7310-1*	*Philippines
P. hennisianum	*742-1, 742-2, 742-4, 742-7, 731*	*Philippines
P. hirsutissimum	*s.n.* (Live plant of Selby collection)	*Thailand
P. hookerae	*s.n.* (Live plant of Selby collection)	*Borneo
P. insigne	*7323*	*India
P. laevigatum	*758*	*Philippines
P. lawrenceanum	*77187*	*Borneo
P. linii	*744*	*Borneo
P. lowii	*77199*	*Java or Malaya
P. mastersianum	*767-1, 767-2*	*Moluccas
P. niveum	*7615*	*Thailand
P. parishii	*768-1*	*Thailand or Burma
P. philippinense	*77190, 813*	*Philippines
P. praestans	*738*	*New Guinea
P. purpuratum	*735*	*Hongkong
P. randsii	*816*	*Philippines
P. rothschildianum	(Leaf donated by F. L. Stevenson)	* Borneo
P. spicerianum	*7630*	*India
P. stonei	*s.n.* (Live plant in Selby collection)	*Borneo
P. sukhakulii	*7629-1, 7629-3*	*Thailand
P. tonsum	*733*	*Java
P. venustum	*601*	*India
P. victoria-regina		*Sumatra and Java
subsp. *chamberlainianum*	*7641*	
subsp. *liemianum*	*736*	
subsp. *primulinum*	*7610*	
P. villosum (P. dilectum?)	*811* (Originally in collection of W. L. Stern)	*Southeast Asia
P. violascens	*7631-1*	*New Guinea
P. wardii	(Live plant in Selby collection)	*Burma