THE SYSTEMATIC STATUS OF THE GENUS BLETILLA (ORCHIDACEAE)

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ABSTRACT

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by Kiat W. Tan

The genus Bletilla has been variously placed in the major classifications of the Orchidaceae. Some recent systems include it in the tribe Epidendreae, subtribe Arethusinae. This study attempts to provide a better understanding of the relationships of Bletilla and to clarify its systematic position. A survey is provided of the taxonomic assignments of the genus in major classifications of the Orchidaceae, and morphological comparisons are made of species chosen to represent the genera Bletilla, Arethusa, and Bletia. Chromosome numbers reported for Bletilla and Bletia are summarized, and a preliminary report is provided on intergeneric crossing studies. It was found that Bletilla consistently shows greater similarity to Bletia than to Arethusa, and that its relationships can be better understood in light of evolutionary trends in the genus Bletia. It is suggested, therefore, that Bletilla be removed from the subtribe Arethusinae and placed near Bletia in the Bletiinae.

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The Asiatic genus Bletilla was described from a species (Fig. 1) originally placed in the American genus Bletia of the tribe Epidendreae. Subsequent to its description, Bletilla has generally been associated with Arethusa in the tribe Neottieae. Recent authors have removed the Arethusa alliance from the Neottieae to the Epidendreae, once again placing Bletilla in the same tribe with Bletia, although in separate subtribes.

This diversity of treatment is reflective of the complexity of the very large family Orchidaceae with its reticulate relationships within and between groups. The complexity is apparently an outcome of relatively rapid diversification in geologically recent times, and is manifest in the wide variations of growth habits and forms found in the family. Floral morphology in particular has evolved with extremely close relationships between the flowers and their pollinators. This specificity of structure to pollinator has resulted in extreme variation of form ranging from the inconspicuous to the bizarre. Often evolution of the habit of the plants has not kept pace with that of floral morphology, thereby creating much confusion in the taxonomy of the various groups. Nevertheless, one can find excellent evolutionary series for nearly every morphological feature within the orchids. Dressler and Dodson (1960) state:

> As an actively evolving group in which the patterns of evolution are unusually clear,

Figure 1. Flower of *Bletilla striata* f. *gebina*.

> the orchids are especially appropriate for evolutionary study and may throw a good deal of light on parallelism, polyphylesis and other problems which plague the biologist dealing with apparently more ancient groups.

In most classifications of the Orchidaceae, too much importance has been attached to relatively few features or "key characters" which often prove fallible. As a result, closely related genera are separated, thereby obscuring evolutionary trends within the family. This appears to be the case with the genus Bletilla. I believe that Bletilla represents a significant stage in the evolution of the groups in which Arethusa and Bletia have been classified. Bletilla exhibits many characters in common with Arethusa and Bletia, but the similarity to Bletia is especially striking. Although Bletilla has been more closely associated with Arethusa than with Bletia in recent classifications, the constantly more primitive nature of the characters of Bletilla can be better understood in the light of evolutionary trends in the large and variable genus Bletia.

This study was designed therefore to provide a better understanding of the relationships of Bletilla and to clarify its systematic position. It includes a survey of the taxonomic assignments of the genus in the major classifications of the Orchidaceae, a morphological comparison of species chosen to represent the genera Bletilla, Arethusa and Bletia, a review of chromosome numbers reported for

Bletilla and Bletia, and crossing experiments designed to test intergeneric affinities.

SURVEY OF PREVIOUS TAXONOMIC ASSIGNMENTS OF THE GENUS BLETILLA

The concept of the genus was first recognized and treated by Rafinesque in 1836 under the name Jimensia. Reichenbach fil. described the genus again in 1853, naming it Bletilla for the resemblance to Bletia Ruiz & Pav.. This name was subsequently conserved (Lanjouw et al., 1961).

Reichenbach's description was based on a species that Lindley (1847) had named Bletia Gebina and had placed in the tribe Epidendreae. Reichenbach considered Bletilla to be closely allied to Arethusa in the tribe Arethuseae. He included the Arethuseae with the Epidendreae in the Euoperculatae. Bletilla was again included in the genus Bletia by Bentham (1883) who emphasized the structure of anther and pollinia for tribal delimitation. In Genera Plantarum, he treated it as a section of the genus Bletia in the tribe Epidendreae.

Pfitzer (1889), who prepared the Orchidaceae in Engler & Prantl's "Die natürlichen Pflanzenfamilien", emphasized the importance of vegetative characters in orchid classification. He placed Bletilla apart from both Arethusa and Bletia as follows:

a. Monandrae
Acranthae
Articulatae
Thuniinae
Bletilla

b. Monandrae
Acranthae
Convolutae
Pogonieae
Arethusa

c. Monandrae
Acrotonae
Pleuranthae
Convolutae
Homoblastae
Phajinae
Bletia.

The most widely accepted system of classification is that of Schlecter (1926) who based his scheme on Pfitzer's classification, but also made use of the reproductive structures emphasized by Bentham (following Lindley). In this classification, *Bletilla* was once again associated with *Arethusa* in the same subtribe, while *Bletia* was placed in a separate tribe altogether, i.e.:

a. Monandrae
Acrotonae
Polychondreae
Bletilleae
Bletilla
Arethusa

b. Monandrae
Acrotonae
Kerosphaereae
Pleuranthae
Sympodiales
Phajeae
Bletia

The wide acceptance of Schlecter's system has apparently deterred research on the classification of the orchids, with the result that few attempts have been made to present a more satisfactory classification until recently. Mansfeld (1937, 1955), who regarded Schlecter's system as a natural one, reviewed it and made some modifications. One of these was the removal of the subtribe Bletillinae (which includes

both Arethusa and Bletilla) from the Neottieae (Schlecter's Polychondreae) to the Epidendreae. This united Bletilla, Arethusa and Bletia in the same tribe, although Bletia was placed in a separate subtribe, the Phaiinae. More recently, Dressler and Dodson (1960) evaluated Schlecter's system and proposed a classification in which the nomenclature was brought in accordance with present rules, and with several changes made in arrangement and circumscription. In this classification, the subtribe Arethusinae (Bletilleae Schltr.) was placed next to the subtribe Bletiinae (Phajeae Schltr.) within the tribe Epidendreae. The relation between these three genera was recognized, although Bletilla was presumed to be closer related to Arethusa in this arrangement. In an even more recent system of the family, Vermeulen (1966) recognized two tribes, Neottianthae and Epidendranthae in the subfamily Epidendroideae. The tribes are equivalent to Reichenbach's Neottiaceae and Euoperculatae respectively, with the exception that while Reichenbach f. included the Arethuseae in the Euoperculatae, Vermeulen considered most of the Arethuseae to belong in the Neottianthae. However, he noted:

> The genera Sobralia and Bletilla (and some related genera) have granular pollen, but on account of their general habit they are classified among the Epidendranthae.

The foregoing survey shows that the genus Bletilla has been variously placed in the major classifications of the Orchidaceae, with a recent trend for placing it in close

association with both Arethusa and Bletia. The diversity of treatment is in part due to the complexity of the orchid family. The two-dimensional perspective of a standard classification imposes a severe limitation in the representation of a rapidly evolving group with its series of evolutionary lines radiating in various directions to form a three-dimensional reticulum of inter- and intrageneric relationships. Furthermore, the systems of classifications generally have been based on relatively few "key characters", none of which are infallible. Despite the use of different characters which resulted in some differences in circumscription, three main groups recur in the classifications by the different authors of orchids with a single fertile anther (Orchidoideae). They are: the Epidendreae Lindley (Malaxeae Lindley, Vandeae Lindley, Euoperculatae Reichb. f., Pfitzer's tribes, Kerosphaereae Schltr., Epidendranthae Vermln.), the Neottieae Lindley (Acranthae-Convolutae Pfitzer, Polychondreae Schltr., Neottianthae Vermln.), and the Orchideae Dressl. & Dods. (Ophrydeae Lindley, Basitonae Pfitzer). Of these three groups, the Orchideae appear to be the best circumscribed, while distinction between the other two is less clear. No single character can be employed for a sharp, diagnostic separation of the two groups without splitting natural genera and subtribes. The Arethusinae Bentham (Bletilleae Schltr.) appears to be a transitional group with genera bearing characters diagnostic for both the Neottieae

and the Epidendreae. The genera included in the Arethusinae (Dressler and Dodson, 1960) are Arethusa, Calopogon, Crybe and Bletilla. Crybe has been reduced to a synonym of Bletia (Dressler, 1964). Calopogon shares many features with Bletia, and the evidence from further study may require its removal from the Arethusinae. The present study is concerned with the genus Bletilla which, according to Dressler and Dodson (1960), may well be more closely related to Bletia than to Arethusa.

Table 1 presents a survey of the major subdivisions of the Orchidoideae according to the various classifications. The assignments of Bletilla, Arethusa and Bletia by the different authors are indicated in the table.

METHODS AND MATERIALS

This study was based primarily on living plants, but limited reference has been made also to herbarium specimens and material in liquid preservatives. Fresh materials are important in orchid research because some structures of the flowers, especially the viscidia, caudiculae and pollinia, are so altered by preservation that they cannot be properly interpreted. Use of living material has also facilitated observations on growth and development of the plants.

During the winter of 1967, 12 rhizomatous corms of Bletilla striata and 12 of B. striata f. gebina (under the

Table 1. Survey of the major subdivisions of the Orchidoideae

AUTHOR	MAJOR GROUPS			
LINDLEY (1830-1840)	1. Malaxeae 2. Epidendreae △	3. Vandeae	5. Arethuseae ■ 6. Neotteae	4. Ophrydeae
BENTHAM (1883)	1. Epidendreae △	2. Vandeae	3. Neottieae ■	4. Ophrydeae
REICHENBACH FIL. (1852)	II. Operculatae 2. Euoperculatae ▲ ● ■		1. Neottieae	I. Ophrydeae
PFITZER (1888)	II. Acrotonae Acranthae: Duplicatae Articulatae ▲ Pleuranthae: Convolutae ● Duplicatae		Acranthae: Convolutae ■	I. Basitonae
SCHLECTER (1926)	II. Acrotonae 3. Kerosphaereae: Acranthae Pleuranthae ●		2. Polychondreae ▲ ■	I. Basitonae 1. Ophrydoideae
MANSFELD (1937, 1954)	II. Kerosphaerae 3. Epidendreae ▲ ● ■	4. Vandeae	I. Thrauosphaerae 1. Neottieae	2. Ophrydeae
DRESSLER & DODSON (1960)	3. Epidendreae ▲ ● ■		1. Neottieae	2. Orchideae
VERMEULEN (1965)	II. Epidendroideae 2. Epidendranthae ▲ ● ■		1. Neottianthae	I. Orchidoideae

△ Bletilla included in Bletia ▲ Bletilla ● Bletia ■ Arethusa

commercial names of Bletilla hyacinthina and B. hyacinthina 'Alba') of Japanese origin were purchased from Oakhurst Gardens, Arcadia, Calif. These were potted in March and placed in a greenhouse. Budding plants were later placed in a growth chamber for closer observation. By the middle of May, four plants came into flower. Two more plants came into flower, with the last flower fading by the first week of June. Individual plants, producing from 2-5 flowers, remained in flower for a period of 4-8 days.

Plants of Arethusa bulbosa (Tan 28, 29, MSC) in bud and flower were collected from a sphagnum bog in Allegan Co., Michigan, R 15 W, T 3 N, sect. 27, SE 1/4, on May 27, 1967. The plants were potted in living sphagnum and placed in a growth chamber set for 12 hours of incandescent and fluorescent light concurrently, nighttime temperature 72°F. and daytime temperature of 78°F.

Fresh flowers of Bletia catenulata were supplied by Dr. C. H. Dodson, University of Miami, from a collection originally from Tingo Maria, Peru. Pseudobulbs and fresh flowers of Bletia purpurea were provided by Miss C. R. Broome, University of South Florida. Material grown from the pseudobulbs and a potted plant of B. catenulata on loan from Margaret Ilgenfritz Orchids, Monroe, Michigan had not come into flower after 3 months of culture, but these plants were useful in the study of vegetative and developmental features.

Intergeneric crosses involving Arethusa bulbosa, Bletia catenulata, B. purpurea, Bletilla striata and B. striata f. gebina were made by manual transfer of pollinia using forceps and tooth-picks. Crosses were also carried out by Dr. W. P. Stoutamire, University of Akron, with his own plants. Some of the pollinia of Bletia catenulata and B. purpurea used in the crosses were provided by Drs. Dodson and Stoutamire and Miss Broome.

Voucher specimens of plants grown to flowering at Michigan State University are filed in the Beal-Darlington Herbarium of Michigan State University. The collections of Bletilla in the U. S. National Herbarium and representative specimens of Bletia and Arethusa in the Beal-Darlington and University of Michigan herbaria were examined.

The line drawings were made from fresh and preserved material. The photomicrographs of pollinia were taken with a Zeiss dissecting microscope and Exacta attachment camera.

MORPHOLOGICAL COMPARISONS

The comparisons of Bletilla, Arethusa and Bletia have been made on the basis of selected species, including the type species, of each genus. Bletilla includes about 11 species, most of which were described by Schlecter (1911). Bletilla gebinae (Lindl.) Rchb.f. (= B. striata (Thunb.) Rchb. f. forma gebina (Lindl.) Ohwi), the type species of the genus, was used in this study. It is widely distributed

in Japan, Formosa, south-central China and Tibet. In Japan it grows on grassy slopes in foothills (Ohwi, 1965) and in boggy depressions in fields (Charette 1122, US). In China Steward et al. 165, Steward 2603, and Ching 1326 (all US) were collected on grassy slopes. One species of Arethusa, A. bulbosa L. was utilized. This is the type species of the genus, and is also the only undisputed species of Arethusa. It is restricted to temperate and boreal eastern North America where it occurs mostly in sphagnum bogs and peaty meadows. The genus Bletia is a large one with about 50 species distributed in tropical and subtropical America. Bletia catenulata Ruiz & Pav. is the type species. It and B. purpurea (Lam.) DC. were used in this study. The latter is the only species in the genus native to the United States, where it is frequent in southern Florida on grassy hills, wet cliffs, on rocks in dry woods and fields, and in pine barrens.

1. Bletilla striata (Thunb.) Rchb.f.

Erect terrestrial herb; corm rhizomatous, pseudobulbous at the base of the season's shoot, beneath surface level; roots numerous, fleshy, fasciculate at the base of the developing corm. Leaves 4-6, convolute in bud, developing at the time of flowering, plicate, articulate, elliptic-lanceolate to oblong, lower leaves sheath-like. Inflorescence terminal

on a leafy shoot, racemose, 2-5 flowered; floral bracts with scarious margins, 2-3 cm long, 6-8 mm wide, acute, caducous.

Flowers showy, rose-purple (white forms = B. striata f. gebina), petals and sepals nearly equal, ascending, 2.5-3.5 cm long, 6-10 mm wide; labellum free to the base of the column, as long as the other perianth parts, strongly 3-lobed; terminal lobe suborbicular, slightly recurved, with undulate margins and 5 parallel ridges confined to the inner surface and extending to the base of the throat; lateral lobes elliptic, incompletely enfolding the column. Column slightly arching, with two slender wings, shorter than the perianth segments, 1.5-2 cm long, 3.5-4.5 mm wide near the apex; clinandrium present; anther operculate, incumbent; filament very short; pollinia 4, more or less bilobed, laterally compressed in two pairs, one in each cell of the anther, mealy, with tetrads united by elastic strands of tapetal origin; rostellum large, arching over the stigmatic cavity. Figures 1 and 2.

Description based on Tan 1, 4, 10, 13, 21 and 22.

2. Arethusa bulbosa L.

Low terrestrial herb; corm bulbous, smooth, beneath surface level; roots few, slender, fleshy, fasciculate at the base of the developing shoot. Leaf single (rarely 2), convolute in bud, developing as the capsule matures, grass-

Figure 2. Bletilla striata: (a) petals and sepals; (b) labellum; (c) attachment of labellum; (d) column; (e) pollinia from one cell of anther; (f) apex of column, dorsal view; (g) apex of column, ventral view; (h) apex of column, frontal view.

Figure 3. Arethusa bulbosa: (a) petals and sepals; (b) labellum; (c) attachment of labellum; (d) column; (e) pollinia from one cell to anther; (f) apex of column, dorsal view; (g) apex of column, ventral view; (h) apex of column, frontal view.

like, linear-lanceolate; sheaths 2-3, lightly inflated, scarious. Inflorescence terminal on a leafy shoot, scapose, single-flowered (rarely 2-flowered); floral bracts minute, persistent, or absent.

Flowers very showy, rose-purple (occasional white forms occur), perianth segments obliquely attached at the summit of the ovary; sepals and petals subequal, connivent, arched over the column forming a hood; dorsal sepal linear-oblong, obtuse, 3-5 cm long, 5-10 cm wide; lateral sepals falcate, broadly oblong-lanceolate, 2.5-4.5 cm long, 6-9 mm wide; labellum large and showy, unlobed to obscurely 3-lobed, strongly arcuate-recurved, shallowly crenulate or erose along the margins, veins crested with fimbriate, fleshy tissue, basal portion adherent to the column forming a vertical tube with a nectary sac at the base. Column strongly arching, compressed, flaring into an apical wedge with wings tapering abruptly from the apex, 2.5-3.5 cm long, 8-12 mm wide at the apex, 4-6 mm wide below the apex; clinandrium not distinct, anther bed represented by a very slight depression; anther incumbent, operculate, the locular opening hidden by the rostellum, attached to the column by a very short filament, containing 4 boat-shaped pollinia, 2 in each cell; pollinia sectile, soft, consisting of pollen tetrads united into granular masses interconnected by tapetal strands; rostellum broad, arching over the stigmatic cavity and separating it from the locular opening of the anther. Figure 3.

Description based on Tan 28, 29.

3. Bletia catenulata Ruiz & Pav.

Terrestrial or semiterrestrial herb; pseudobulbs subglobose, epigeal and green, with several nodes; roots numerous, velamentous, in a fascicle at the base of the new shoot. Leaves two to several, convolute in bud, developing after flowering, plicate, articulate, fugacious with the persistent leaf-bases crowning the apex of the pseudobulb, elliptic-lanceolate, lower leaves sheath-like. Inflorescence a scapose raceme, lateral on the pseudobulb, many-flowered; bracts small, acuminate, persistent.

Flowers very showy, rose-purple; equal, oblong-lanceolate, 3-3.5 cm long, 10-13 mm wide; petals about as long as but twice as wide as the sepals; labellum free to the base of the column, slightly longer than the petals, strongly 3-lobed; terminal lobe deeply notched, reniform, with entire margins, 3 parallel ridges on the inner surface extending to the base of the throat, with a network of veins radiating from the ridges; lateral lobes ovate and spreading. Column slightly arching, with two rounded wings at the apex gradually tapering to the base, 1.6-2.2 cm long, 6-7 mm wide at the apex, 4-5 mm wide along the rest of the length, slightly biauriculate at the base; clinandrium distinct; anther operculate, incumbent, filament very short; pollinia 4, subdivided into 8 half-pollinia which are ovate, laterally compressed and connected in pairs by caudiculae largely com-

posed of elastic tapetal strands, soft, with tetrads closely united by tapetal strands; rostellum large, slightly arching over the stigmatic cavity. Figure 4.

Description based on flowers provided by Dr. C. H. Dodson, and a potted plant on loan from Margaret Ilgenfritz Orchids.

4. Bletia purpurea (Lam.) DC.

Terrestrial or semiterrestrial herb; pseudobulbs subglobose, epigeal and green, with several nodes; roots numerous, heavily velamentous, in a fascicle at the base of the new shoot. Leaves 2-several, convolute in bud, developing after flowering, plicate, articulate, fugacious, elliptic-lanceolate, lower leaves sheathlike. Inflorescence a scapose raceme or panicle, lateral on the pseudobulb, 1-many-flowered; bracts small, acute, persistent.

Flowers showy to cleistogamous, rose-purple to nearly white; sepals subequal, 2-2.5 cm long, 5-8 mm wide, lateral sepals obliquely ovate-oblong and somewhat connivent and gibbous at the base; dorsal sepal ovate-lanceolate; petals folded over the column to form a hood, ovate-oblong, concave, 1.5-2.5 cm long, 7-11 mm wide; labellum free to the base of the column, nearly as long as the petals, strongly 3-lobed; terminal lobe suborbicular, with undulate-crenate margins, 5-7 parallel ridges on the inner surface extending

Figure 4. Bletia catenulata: (a) petals and sepals; (b) labellum; (c) attachment of labellum; (d) column; (e) pollinia from one cell of anther; (f) Apex of column, dorsal view; (g) Apex of column, ventral view; (h) Apex of column, frontal view.

Figure 5. Bletia purpurea: (a) petals and sepals; (b) labellum; (c) attachment of labellum; (d) column; (e) pollinia from one cell of anther; (f) Apex of column, dorsal view; (g) Apex of column, ventral view; (h) Apex of column, frontal view.

to the base of the throat; lateral lobes incurved, broadly rounded at the base, tapering to a triangular-obtuse apex. Column falcate, with two rounded wings at the apex gradually tapering to the central portion and widening again to two basal wings, 1.2-1.5 cm long, 4-5 mm wide at the wings; clinandrium distinct; anther operculate, incumbent; filament very short; pollinia 4, subdivided into 8 half-pollinia which are ovate, laterally compressed and connected in pairs by caudiculae largely composed of elastic tapetal strands, waxy, with tightly packed pollen tetrads; rostellum large, slightly arching over the stigmatic cavity. Figure 5.

Pseudobulbs and flowers provided by Miss C. R. Broome. Description based on these flowers and plants raised from the pseudobulbs.

Discussion. The habit and growth of Bletilla striata and the two species of Bletia examined are strikingly similar, while those of Arethusa bulbosa are less so. Except for the pseudobulbs, the vegetative portions of the Bletia species resemble those of Bletilla striata very closely. The underground perennating structures of Bletilla appear to be a form from which the pseudobulb of Bletia might have been derived. There is a wide range in the form of perennating structures in the genus Bletia, and the swollen portion of the stem of some species is half-covered to totally covered by soil. In the latter case, the structure is similar

to the pseudobulbous swelling at the base of the shoot of Bletilla striata. The heavily velamentous roots of Bletia purpurea resemble those of epiphytic orchids. According to Correll (1950), Bletia purpurea has been seen growing on rock ledges with half the length of its roots trailing over bare rock, and the other half lightly threading the surrounding loose litter. This prompted him to suggest the descriptive term "semiterrestrial". The development of velamen on the roots and the formation of epigeal pseudobulbs reflect a trend toward the epiphytic habit from the truly terrestrial habit represented in Bletilla striata. The position of the inflorescence has been used by some authors for separating Bletia from the other two genera. However, some species of Bletia appear to have inflorescences terminal on a leafy shoot as in Bletilla striata and Arethusa bulbosa, while an herbarium specimen (Henry 11120, US) and an illustration of Bletilla sinensis (Rolfe) Schltr. (Bot. Mag. 130: Tab. 7935. 1904) show distinctly lateral inflorescences on leafy shoots. The inconsistency of this character, wherein both terminal and lateral inflorescences may be displayed by closely allied genera or even by the same genus raises the question of the validity of this character as a significant feature in orchid classification (Hirmer, 1920; Mansfeld, 1955). Arethusa bulbosa does not resemble the other two genera very closely in its vegetative morphology, but has more features in common with Bletilla striata than

with Bletia catenulata or B. purpurea (Table 2). The differences probably can be explained as adaptations to its unusual and specific habitat. For instance, it has a white underground corm as does Bletilla striata. However, the new corm develops as a bulbous swelling at some point on the stem above the old corm, apparently as an adaptation for maintaining the new corm at the same depth in the growing sphagnum mat while the old corm withers. It has an inflorescence terminal on a leafy shoot as in Bletilla striata, but unlike the latter, it has only a single flower (rarely two). Also unlike Bletilla striata, Bletia catenulata and B. purpurea, Arethusa bulbosa usually has a single, grass-like, nonarticulate leaf, and only a few slender and succulent roots. It is interesting to note that Calopogon, the only other genus in the subtribe Arethusinae besides Arethusa and Bletilla, occurs in similar, and quite often the same habitats as Arethusa bulbosa, and shares certain features with Arethusa (white ellipsoid corm; 1-2 grasslike leaves; 1-2 sheathing, scarious, somewhat inflated bracts; fleshy, succulent roots).

A comparison (Table 2) of the floral morphology of Bletilla striata, Arethusa bulbosa, Bletia catenulata and B. purpurea reveals features common to all three genera. In general, however, Bletilla striata again shows a closer resemblance to the two species of Bletia than to Arethusa bulbosa. The floral envelope and the column structure of

Table 2. A summary of the comparative morphological features of species of *Bletilla*, *Arethusa* and *Bletia*.

	Bletilla striata and *B. striata* f. *gebina*	*Arethusa bulbosa*	*Bletia catenulata* and *B. purpurea*
Habit	Erect terrestrial herbs	Low terrestrial herbs	Terrestrial to semi-terrestrial herbs
Perennating structure	Rhizomatous corm, pseudobulbous at base of new shoot, hypogeal	Bulbous corm, hypogeal	Variable, rhizomatous corm to pseudobulb, hypogeal to epigeal
Roots	Numerous, fleshy, fasciculate	Few, slender, fasciculate	Numerous, velamentous, fasciculate
Leaves	4-6, convolute in bud, developing at the onset of flowering, plicate, articulate	1 (rarely 2) convolute in bud, developing after flowering, grasslike, nonarticulate	2- several, convolute in bud, developing after flowering, plicate, articulate
Inflorescence	Terminal on a leafy shoot, racemose, 2-8 flowered	Terminal on a leafy shoot, scapose, 1-flowered (rarely 2)	Lateral on pseudobulb to terminal on leafy shoot, scapose raceme or panicle, 1-many-flowered
Sepals and petals	Nearly equal, ascending	Subequal, connivent to form a hood over the column	Subequal, ascending to closed

. . . continued

Table 2 (continued).

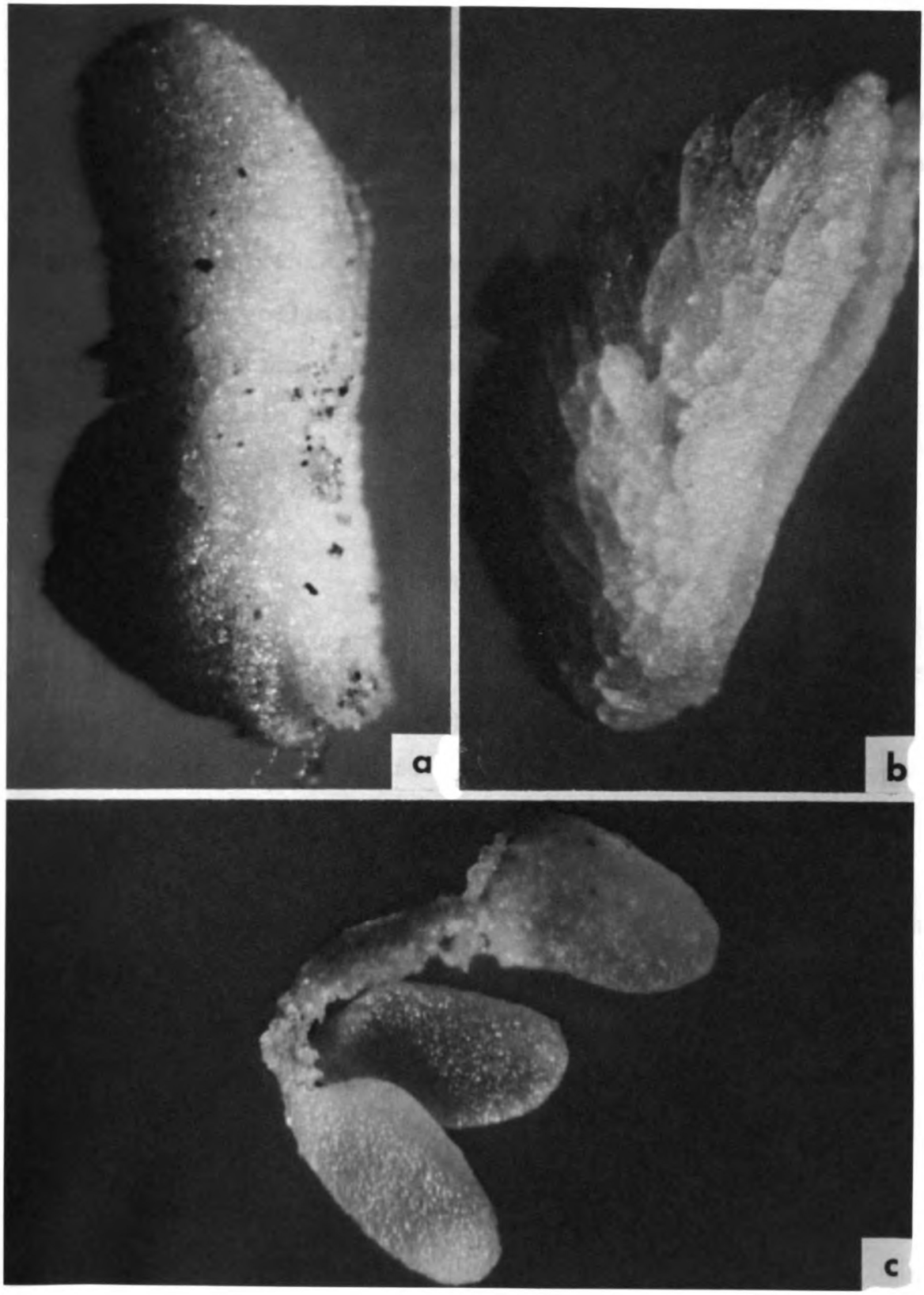
	Bletilla striata and *B. striata* f. *gebina*	*Arethusa bulbosa*	*Bletia catenulata* and *B. purpurea*
Labellum	Free, 3-lobed, 5 parallel ridges on inner surface	Adnate to column at base, unlobed to obscurely 3-lobed, fimbriations on inner surface	Free, 3-lobed, 5-7 parallel ridges on inner surface
Column	Slightly arching, winged	Strongly arching, compressed, wedge shaped at apex	Slightly arching to falcate, winged at apex and base
Clinandrium	Present	Obscure	Present
Anther	Operculate, incumbent, attached by short filament	Operculate, incumbent, attached by short filament	Operculate, incumbent, attached by short filament
Pollinia	4, more or less bilobed, mealy	4, boat-shaped, sectile	8 half-pollinia, soft to waxy
Rostellum	Prominent	Prominent	Prominent

Bletilla and Bletia are relatively similar, while Arethusa appears to have more specialized flowers, with its obliquely attached perianth segments arching to form a hood over the column, its fimbriated, unlobed lip, its tubular structure and pouch formed by the adnation of the column to the basal portion of the lip, its compressed and arcuate column with a wedge-shaped apex, and by the absence of a distinct clinandrium. The attachment and position of the anther is the same in the three genera, but is larger in relation to the stigmatic cavity in Bletilla striata and Arethusa bulbosa than in the two species of Bletia.

The nature of the pollinia is the prime character used in separating the subtribe Arethusinae from the subtribe Bletiinae. The consistency and texture of the pollinia, however, differ in all the species of the three genera that were studied. The pollinia of Bletilla striata (Fig. 6a) are kidney-shaped with separated or incompletely separated lobes, so that there are four pollinia, two in each cell of the anther. The consistency of these pollinia is mealy, with the pollen tetrads loosely united by elastic tapetal strands to form soft, coherent masses. Each Bletia pollinium (Fig. 6c) is divided into two half-pollinia connected by a caudicula largely composed of viscid tapetal strands. The anther therefore contains eight half-pollinia which are ovate and laterally compressed. The pollen tetrads are more closely packed than those of Bletilla striata or

Arethusa bulbosa. In many species of Bletia, including B. purpurea, the tetrads are so tightly packed that the half-pollinia appear waxy. Other species of Bletia, however, have pollinia which range in consistency from soft to cartilaginous. For example, Bletia stenophylla Schltr. is reported to have soft pollinia (Dunsterville & Garay, 1959-66). The pollinia of Bletia catenulata are fairly soft in the fresh flower. When removed from the flower and refrigerated, however, they developed a hardness approaching that of waxy pollinia. Pollinia left on the flower became mealy as germination was initiated. It would therefore appear that the state of freshness determines to some extent the consistency of the pollinia, and pollinia of dried specimens appear more "waxy" than when they are fresh. The texture of Bletilla striata pollinia resemble Bletia pollinia more closely than those of Arethusa, even though Bletia pollinia appear harder. The resemblance is greatest in species of Bletia with soft pollinia where the term "mealy" appears appropriate. On the other hand, although the pollinia of Arethusa bulbosa (Fig. 6b) are as soft as Bletilla striata pollinia, and break down as readily, the sectile nature clearly differentiates them. Arethusa bulbosa has 4 boat-shaped pollinia in the anther, 2 in each cell. Each pollinium is made up of pollen tetrads united into granular masses, and these masses are interconnected by tapetal threads. Although the granular masses are not as distinct as in members of the tribe

Figure 6. Pollinia of (a) Bletilla striata; (b) Arethusa bulbosa; and (c) Bletia purpurea (all X64).


a
b
c

Orchideae, the term "sectile" is applicable. It is again interesting to note that the pollinia of Calopogon are very similar to those of Arethusa. The greater coherence of the pollen tetrads and the separation of the pollinium lobes into 2 half-pollinia connected by a distinct caudicula suggest that the pollinia of Bletia represent a more advanced stage of evolution than those of Bletilla striata. The Arethusa pollinia appear to represent a separate trend of development.

CYTOLOGY

For a family as large as the Orchidaceae, the proportion of chromosome counts reported thus far is very small. No counts are available for Arethusa bulbosa, and only one count has been published for Bletia (Blumenschein, 1960). However, counts for some species of Bletilla have been reported by Afzelius (1943) and Miduno (1938-1940). The counts for Bletilla and Bletia are presented in Table 3. Insufficient counts have been reported to allow a meaningful cytological comparison of the three genera.

Table 3. Chromosome numbers of *Bletilla* and *Bletia*.

Taxon	n	2n	Reported by
Bletilla formosana Schltr.		36	Miduno, 1938
B. formosana Schltr.	18		Miduno, 1940
B. hyacinthina (J.E.Smith) R.Br. (=*B. striata* (Thunb.) Rchb.f.)	16		Afzelius, 1943
B. striata Rchb.f.	16		Miduno, 1938
B. striata Rchb.f.		32	Miduno, 1940
B. striata Rchb.f. var. *gebina* Rchb.f. (=*B. striata* Rchb.f. forma *gebina* (Lindl.) Ohwi)		32	Miduno, 1938
B. striata Rchb.f. var. *gebina* Rchb.f.	16-21		Miduno, 1940
B. striata Rchb.f. var. *albomarginata* Makino		32	Miduno, 1938
Bletia rodriguesii Cogn.		40	Blumenschein, 1960

CROSSING EXPERIMENTS

In the Orchidaceae wide matings often result in fertile progeny. According to Dressler and Dodson (1960), interfertile genera should not be placed in separate subtribes. With this in mind, inter- and intrageneric crosses involving Bletilla, Arethusa, and Bletia were made (Table 4). Crosses utilizing Bletia purpurea as the seed parent were made with a cleistogamous form (Stoutamire 6689). In this case, an attempt was made to avoid contamination by using unopened buds with the pollinia removed.

The results are presently incomplete. Where fertile seed are produced, they will have to be germinated in order to determine whether true hybrids have been formed. The seeds formed from the cross between Bletia purpurea and Arethusa bulbosa may have been a result of selfing since pollen grains were found germinating on the stigmas of several flowers that were opened. The seeds of the cross between Bletia purpurea and Bletilla striata were infertile, but the fact that seeds were formed at all may be significant, since according to Duncan (1959), matings between members of Schlecter's Kerosphaereae and Polychondreae have not been reported if, indeed, they ever have been previously attempted.

Table 4. Inter- and intrageneric crosses involving *Bletilla*, *Arethusa* and *Bletia*.

Date	Cross	Result
5/20/67	*Arethusa bulbosa* X *Bletilla striata* a/	Green fruit with little enlargement. August 4, 1967.
6/6/67	*Arethusa bulbosa* (Tan 28) X *Bletilla striata* (Tan 10)	Capsule developing for about a week, then falling off.
5/20/67	*Bletia purpurea* (Stoutamire 6689) X *Arethusa bulbosa* a/	Seed collected July 19, 1967. Mature flower of *Bletia* used, so selfing may have occurred. Seeds with about 25% containing embryos.
5/20/67	*Bletia purpurea* (Stoutamire 6689) X *Bletia catenulata* (from Dodson) a/	Capsule started to develop, but falling off soon after.
6/3/67	*Bletilla striata* (Tan 10) X *Arethusa bulbosa* (Tan 28)	Green fruit developing. August 4, 1967.
5/16/67	*Bletilla striata* f. *gebina* (Tan 22) X *Bletia catenulata* (from Dodson)	Green fruit developing. August 4, 1967.

a/ Crosses made by W. P. Stoutamire at Akron, Ohio.

CONCLUSIONS

The frequent association of the genus Bletilla with Arethusa and Bletia in the major classifications of the Orchidaceae might be taken as an indication of close relationship between the three genera. This relationship is further suggested by morphological investigations which reveal several features in common among the three genera. Preliminary results from intergeneric crosses also suggest a close relationship. Recent classifications place Bletilla in closer association with Arethusa in the subtribe Arethusinae than with Bletia, subtribe Bletiinae. Morphological comparisons (Table 2) of species of the three genera, however, reveal that while the similarities are greater between Arethusa and Bletilla than between Arethusa and Bletia, the genus Bletilla clearly has more in common with Bletia than with Arethusa. The vegetative and floral structures of the species of Bletilla and Bletia studied consistently showed greater similarity, while those of Arethusa appear specialized toward a particular habitat. Furthermore, some of the characters which have been used for associating Bletilla with Arethusa rather than with Bletia prove to be inconsistent or invalid. Inflorescence position, which has been used by some authors as a major distinguishing character, does not separate Bletilla from Bletia because of transitional forms present in different species of Bletia. The most important and most generally employed character for separating

the Arethusinae from the Bletiinae is the nature of the pollinia. Detailed examination of fresh pollinia of species of the three genera (Fig. 6) reveal that not only are the sectile pollinia of Arethusa very different from the mealy pollinia of Bletilla, but Bletilla pollinia also bear a similarity to pollinia of certain species of Bletia. The degree of hardness has been used to separate Bletia from Bletilla, but some species of Bletia have pollinia almost as soft as Bletilla pollinia.

Finally, it should be noted that while most of the characters of Bletilla resemble those of Bletia, those that do not consistently appear to be more primitive (e.g. non-velamentous roots, underground corm, undivided pollinia) than those present in Bletia. Moreover, on the basis of herbarium specimens and species descriptions, it appears that a series of transitional characters occur in different species of Bletia which bridge the gap between the more primitive structures of Bletilla and the structures found in the more advanced species of Bletia.

Bletilla, Arethusa and Bletia probably evolved from some common ancestral stock possessing features similar to those found in Bletilla today. While the genus Bletilla remained relatively unchanged from the ancestral forms in the temperate regions of Asia, the genus Bletia underwent rapid diversification in tropical and subtropical America in response to the development of the epiphytic habit. The

genus Arethusa, on the other hand, represents a separate adaptive trend for unusual habitats of low pH and high organic matter. On the basis of the morphological comparisons which show Bletilla to be closer to Bletia, I conclude that retention of Bletilla in the subtribe Arethusinae would tend to obscure the evolutionary ties existing between Bletia and Bletilla. Therefore, the genus Bletilla should be transferred to the subtribe Bletiinae.

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