ISSN 0386-5304
No. 5 Dec. 1982

Bulletin of
The Hiroshima Botanical Garden

Published by

The Hiroshima Botanical Garden
(Municipal)
Kurashige, Itsukaichi, Hiroshima
Japan

CONTENTS

目次

A revision of the genus *Paphiopedilum* (Orchidaceae)*

Kohji Karasawa** and Kamezo Saito***

パフィオペディルム属の再検討

唐澤耕司・斉藤亀三

Introduction and History

The genus *Paphiopedilum* is the largest genus including more than 53 species in subfamily Cypripedioideae, and it is one of the well known genera of the Orchidaceae. It is widely distributed in tropical and subtropical regions of East-Asia (from New Guinea to India through Borneo, Java, Sumatra, Malay Peninsula and extending northward to Bhutan, Sikkim and Yunnan of China).

Most species of this genus are growing at highly humid conditions in the tropical and subtropical rain forest, but some are adapting to relatively dried habitats where are often calcareous, rather dried areas. Not only the genus exhibits wide variations in external morphology in many characters and is including various types of species, but also the most species exhibit wide range of morphological variations, especially in the floral characters. The differences in the intraspecific variations are sometimes regarded as the noteworthy criteria of individual plants by the orchid growers as the garden plants. Within the genus, there are also wide variation of chromosome numbers and their karyotypes (Mehlquist 1947, Duncan & MacLeod 1947, 1948, 1949 & 1950, Kamemoto *et al.* 1963, Tanaka & Aoyama 1974, Karasawa 1978, 1979 & 1982, Karasawa & Aoyama 1980, etc.) and the species of this genus are crossed freely in the natural condition (e.g. *P. godefroyae, P. ang-thong,* Karasawa 1979). Moreover, there have been reported many new species in recent time because of the high appreciation of *Paphiopedilum* as the garden plants by orchid growers as well as the close explorations of those areas. This makes the taxonomy of this genus very difficult; the species concept are not well understood, and the genus has been variously classified (Fowlie 1966, Asher 1980–1981, Brieger 1971) without a good understanding of the phylogenetic interrelationships, retaining many ambigous or misunderstood taxa of various ranks in the genus. The present study tries to clarify the taxa, especially the species assemblages above subsection rank, and examine the phylogenetic interrelationships between those taxa as well as to interpretate the inferable speciation lines in those species assemblages.

The name *Paphiopedilum* is date back to Pfitzer (1887) who distinguished the genus from

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* Contribution from the Hiroshima Botanical Garden No. 19.

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Bulletin of The Hiroshima Botanical Garden No. 5: 1–69, 1982.

Table 1. History of classification of *Paphiopedilum* and its related genus.

Hallier 1896	Pfitzer 1903	Asher 1980–1981	Brieger 1971	Karasawa & Saito 1982
COELOPEDILUM APHANONEURA Brachypetalum	BRACHYPETALUM	BRACHYPETALUM	BRACHYPETALUM	PARVISEPALUM
				BRACHYPETALUM
CHROMATONEURA Sigmatopetalum Clinopetalum Drepanopetalum Thiopetalum Ceratopetalum Cymatopetalum Stictopetalum Neuropetalum Pardalopetalum Streptopetalum Mastigopetalum Cochlopetalum	ANOTOPEDILUM Gonatopetalum Coryopedilum Prenipedilum	ANOTOPEDILUM Gonatopetalum Coryopedilum Prenipedilum	POLYANTHA Mastigopetalum Streptopetalum Polyantha Cochlopetalum	POLYANTHA Mastigopetalum Polyantha Mystropetalum
	OTOPEDILUM Mystropetalum Pardalopetalum Cochlopetalum Stictopetalum Neuropetalum Thiopetalum Cymatopetalum Ceratopetalum Spathopetalum Blepharopetalum Phacopetalum	OTOPEDILUM Mystropetalum Pardalopetalum Cochlopetalum Stictopetalum Thiopetalum Neuropetalum Cymatopetalum Ceratopetalum Spathopetalum Venustum Hookerae Mastersianum Blepharopetalum Phacopetalum		COCHLOPETALUM
			PAPHIOPEDILUM Stictopetalum Paphiopedilum	PAPHIOPEDILUM Stictopetalum Paphiopedilum Thiopetalum Ceratopetalum
			BARBATA Sigmatopetalum Blephalopetalum Barbata	SIGMATOPETALUM Spathopetalum Blephalopetalum Punctatum Barbata Planipetalum Sigmatopetalum
PHRAGMOPEDILUM				

Cypripedium (sensu lat.) though the genus had included the species of *Phragmipedium* (sensu str.) at that time (Stein 1892). Subsequently Rolfe (1896) and Hallier (1897) approved Pfitzer's generic concept of *Paphiopedilum.* Hallier (1897) made a further classification of the genus: he classified 56 species into 15 sections of 2 subgenera (Coelopetalum and Phragmopedilum). But the *Paphiopedilum* circumscribed by Hallier (1897) had also included the *Phragmopedilum* (sensu str.), and the subgenus Coelopetalum of Hallier (1897) is corresponding to the strict sense of *Paphiopedilum* and the subgenus Phragmopedilum to the genus *Phragmipedium* (sensu str.). The appropriate circumscription of the genus had been made by Rolfe (1896) and Pfitzer (1903), and they divided the large sense of *Paphiopedilum* into *Paphiopedilum* (sensu str.) and *Phragmopedilum* (sensu str.) by the differences in the number of ovary cells and the detailed morphology of the flower. Pfitzer (1903) recognized 3 subgenera (Brachypetalum, Anotopedilum and Otopedilum) and 15 sections including 47 species. Subdivision of the genus by Pfitzer (1903) had been based only on the differences of floral morphology, and the circumscriptions of those subgenera have been accepted by Fowlie (1966), Asher (1980–81), and some other authors. Another system of the subdivision of the genus had been proposed by Brieger (1971). He, on the basis of the close observations of the herbarium specimens, classified the genus into 4 subgenera (Brachypetalum, Polyantha, Paphiopedilum and Barbata) with 10 sections including 68 species based on the differences of floral morphology, nature of racemes, and leaf morphology. The history of classification is summarized in Table 1.

Acknowledgements

We express our many thanks to Dr. F. Maekawa (Prof. Emer. of University of Tokyo), Dr. R. Tanaka (Prof. of Hiroshima University) for their advice and criticism during this study. Sincere thanks are also due to Dr. H. Ito (Prof. Emer. of Tokyo Kyoiku University) for his helpful suggestions and critical reading of manuscript. We are very grateful to Dr. Tsi Zhanhuo (Institute of Botany, Academia Sinica) and Mr. Satoshi Kimura (Director of Atagawa Toropical Garden & Alligator Farm) for their kindness in placing many important specimens and living plants at our disposal.

Morphology

1. Stem and stolon

In most species of *Paphiopedilum,* the stems are very short and hardly recognizable; In *P. druryi,* exceptionally, the stems are usually elongating to about 10 cm long at native places, and the elongated stems seen under cultural conditions are often observed in some species (e.g. *P. barbatum, P. lawrenceanum*).

In *Paphiopedilum,* there has been reported no species which bears a stolon. Though Tang and Wang (1951) described the occurence of very long rhizome as "rhizomato valde elongato" in the original description of *P. micranthum,* they did not realize the difference between the usual stem and the "very long rhizome". Close observations of herbarium specimens and the living plants revealed that the very long rhizome is not an usual stem but apparently a stolon. We also observed stolons in *P. armeniacum* in the living plants (Fig. 1). In both species, the usual stem which are quite short and less than 0.5 cm long, are extending from the leaf axils of old stem, while the stolons are extending into soil or pot and bearing a young plant at rather distant places from the old stem (Fig. 1). The stolon is shooting out some roots from each underground nodes which is easily recognized by the occurence of a small scale leaf. Thus the stolon observed in both species is well distinguished from the strict sense of stem. The stolon observed in both species is, on the other hand, very similar to the stems of some species of *Cypripedium* (e.g. *C. japonicum*) in appearance. Those stems in *Cypripedium* are extending into soil and forming a dormant bud at tip and shooting out roots from each nodes. The differentiation of stolon in *P. armeniacum* and *P. micranthum* is considered to be one of the transitional form to the temperate, relatively dry habitat where the most deciduous plants are wither out in autumn to winter seasons. And the occurence of stolon in both species seems to be a derived characteristics and one of the noteworthy criteria in the taxonomy of *Paphiopedilum.*

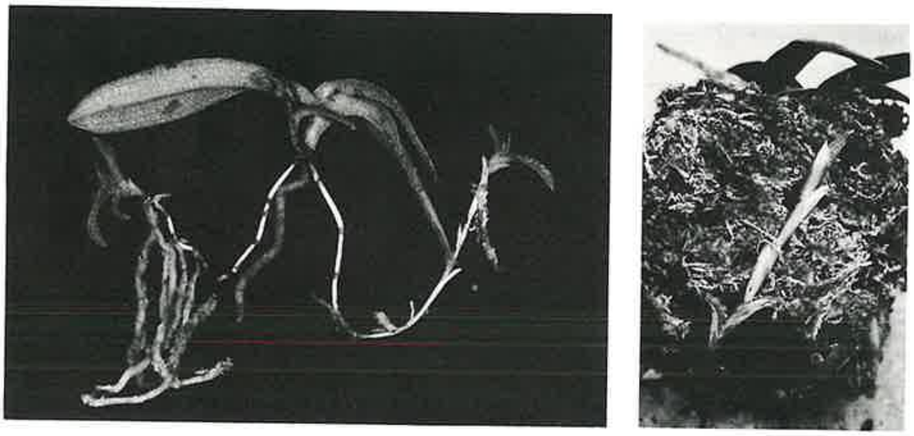

Fig. 1. Stolons of *P. micranthum* (left) and *P. armeniacum* (right).

2. Leaf characters

R.J.V. Delden (1969) made an extensive observations on leaf characters in *Paphiopedilum*, and he stressed on the importance of those features as the key characters in distinguishing the un-bloomed plants of this genus. Atwood & Williams (1978, 1979) made an observation on the fine structure of leaf-surface. The detailed characters of leaves have been precisely appreciated by Brieger (1971) at the first time as the criteria of subgeneric taxonomy of *Paphiopedilum.* Subsequently Karasawa & Aoyama (1981) made a noteworthy observations on the anatomical structures of leaves, and they suggested that the anatomical features of leaves provide us useful criteria in classifying the taxa of *Paphiopedilum.*

The leaves show a great diversity in shape, surface color pattern, marginal cilia, anatomical features (especially the thickness of epidermis, and size and density of stomata), and they seem to provide us important taxonomic characters of various ranks of taxa.

1) External features

The leaves in this genus are all bi-folded and essentially oblong to elliptic in shape (Fig. 2). Though the leaf-shape seems to be rather easily variable under different conditions, there seems to be a following tendency for each subgenus; the leaves in subgenera Parvisepalum, Brachypetalum and Sigmatopetalum are generally shorter and wider than the others and usually oblong to elliptic, while those in subgenera Polyantha, Paphiopedilum and Cochlopetalum are longer and narrower and usually narrow to linear elliptic or oblong.

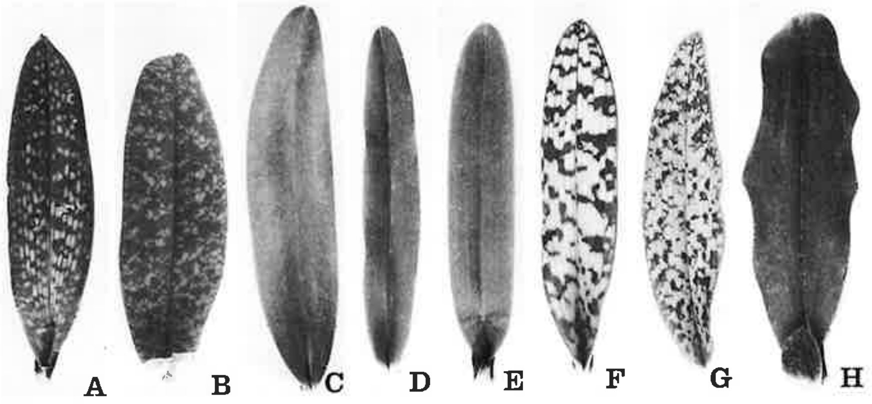

Fig. 2. Variation of leaf-shape and surface marking.
A, *P. micranthum.* B, *P. concolor.* C, *P. haynaldianum.* D, *P. insigne.* E, *P. fairrieanum.* F, *P. lawrenceanum.* G, *P. venustum.* H, *P. liemianum.*

The leaf margin in most species are plain throughout, but the leaves of *P. hookerae* is distinctly dentate as being rough to touch. Fine, white cilia are observed in subgenus Cochlopetalum: the cilia are restricted to the basal margin in *P. victoria-regina,* while they are on the whole margin of the leaves in *P. liemianum.*

There are two extreme types of surface color of leaves in *Paphiopedilum*: the leaves of the species of subgenus Polyantha (sense str.) and Paphiopedilum (sense str.) are pale to deep green and not figured; the leaves of the species of subgenus Parvisepalum, Brachypetalum and Sigmatopetalum are beautifully tessellated with pale to deep, more or less greenish parts and much paler, almost white or greyish parts. The leaves of the species of subgenus Cochlopetalum are very faintly tessellated in appearance, but the color differentiation into deeper parts and paler parts is not distinct in both external appearance and also in anatomical view. The leaves in Cochlopetalum are greyish green, and they, as mentioned above, show the intermediate form between the extreme two types.

The leaf under surface is also classified into two types based on the differences of color pigmentation; the leaves of the species of subgen. Polyantha and of section Barbata of subgenus Sigmatopetalum are mostly not tinged with deep purple color, though the species of rest taxa are usually more or less (partially or entirely) tinged with deep purple color. In the latter type, the leaves of the species of subgenera Parvisepalum and Brachypetalum and *P. venustum* are entirely tinged with deep purple color, while in the other taxa the deep purple color pigmentation is restricted to the basal portion of leaves (Fig. 3).

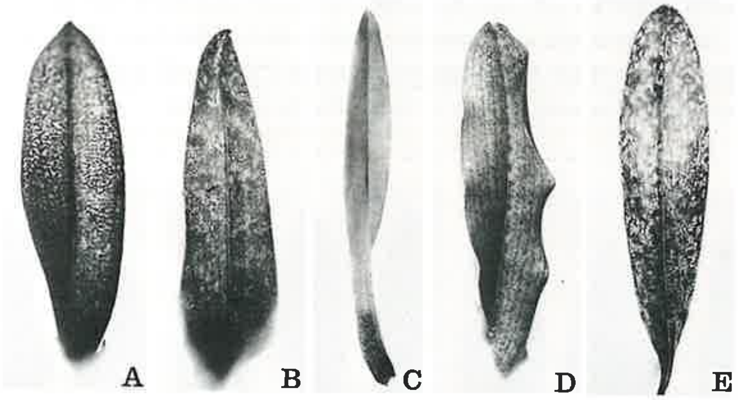

Fig. 3. Color pattern of leaf under surface.
A, *P. micranthum*. B, *P. concolor*. C, *P. villosum*. D, *P. chamberlainianum*. E, *P. venustum*.

The green leaves are commonly seen in Cypripedioideae, but the anthocyan (deep purple) pigmentation on leaf surface and the tessellated or finely figured leaves are observed only in taxa of genus *Paphiopedilum*. The green leaves seem to be apparently a primitive condition, and the presence of anthocyan pigmentation and the tessellated leaves are inferable to be the derived ones. Especially the tessellated leaves are considered to be derived from green leaves in adapting to the rather shady habitats.

2) Anatomical features

Until Karasawa & Aoyama (1981), no close anatomical observation has been made on the *Paphiopedilum* leaves: they made an extensive study on leaves, especially on the anatomical features of *Paphiopedilum* leaves. Their study had concentrated on A) variations of leaf-thickness, B) thickness of leaf-epidermis, C) fine structure of leaf surface, and D) size, shape and density of stomata.

A) Thickness of leaves within this genus is showing a wide variation and vary from 0.47 mm (*P. glaucophyllum*) to 2. 10 mm (*P. parishii*), and it seems to be characteristic for each species (Fig. 4). The variations of leaf-thickness are not so much in most subgenera, which are Parvisepalum (0.70–0.93 mm), Brachypetalum (1.37–1.57 mm), Sigmatopetalum (0.50–0.90 mm) and Cochlopetalum (0.47 0.80 mm), though there are wide variations among the subgenera

Table 2. Thickness of epidermis & mesophyll and size & density of stomata.

Species	Leaf			Stomata	
	Thickness (mm)	Thickness of upper epidermis (mm)	Thickness of mesophyll (mm)	Length of guard cell (μm)	Number of stomata (/mm^2)
armeniacum	0.93	0.27	0.66	56	26.0
delenatii	0.70	0.20	0.50	58	19.1
micranthum	0.86	0.15	0.71	53	27.9
bellatulum	1.57	1.03	0.54	49	40.5
concolor	1.37	0.70	0.67	37	46.5
niveum	1.47	1.00	0.47	43	48.0
elliottianum	1.17	0.40	0.77	44	44.5
philippinense	1.33	0.77	0.56	54	28.5
praestans	1.33	0.70	0.63	55	33.0
randsii	0.95	0.46	0.48	44	40.1
rothschildianum	0.93	0.20	0.73	54	37.1
stonei	0.70	0.11	0.59	52	41.6
haynaldianum	1.07	0.47	0.60	44	40.5
lowii	0.80	0.28	0.52	42	43.5
parishii	2.10	1.27	0.83	47	51.0
hirsutissimum	0.60	0.22	0.38	43	37.5
charlesworthii	0.86	0.35	0.51	38	86.6
exul	1.10	0.60	0.50	49	43.5
insigne	0.65	0.15	0.50	48	63.0
i. var. *sanderae*	0.68	0.15	0.53	50	73.1
villosum	0.70	0.10	0.60	37	40.5
fairrieanum	0.83	0.43	0.40	44	54.0
druryi	1.43	0.73	0.70	48	43.5
spicerianum	0.73	0.23	0.50	45	49.5
appletonianum	0.53	0.10	0.43	63	21.5
bullenianum	0.63	0.20	0.43	57	15.0
mastersianum	0.77	0.12	0.65	63	13.5
violascens	0.63	0.11	0.52	65	22.5
tonsum	0.57	0.13	0.44	61	13.5
argus	0.73	0.25	0.48	65	26.5
barbatum	0.67	0.10	0.57	60	20.5
callosum	0.87	0.22	0.65	65	18.0
lawrenceanum	0.70	0.13	0.57	62	12.0
ciliolare	0.90	0.23	0.67	65	18.5
urbanianum	0.57	0.20	0.37	67	15.0
virens	0.67	0.15	0.52	62	21.0
purpuratum	0.57	0.05	0.52	61	15.0
sukhakulii	0.50	0.10	0.40	60	13.5
venustum	0.80	0.27	0.53	60	15.0
chamberlainianum	0.80	0.23	0.57	50	33.0
c. var. *latifolium*	0.75	0.21	0.54	54	31.5
glaucophyllum	0.47	0.13	0.34	53	27.0
liemianum	0.72	0.20	0.52	57	32.0
l. var. *primulinum*	0.76	0.25	0.51	52	39.0
victoria-regina	0.70	0.13	0.57	60	31.1

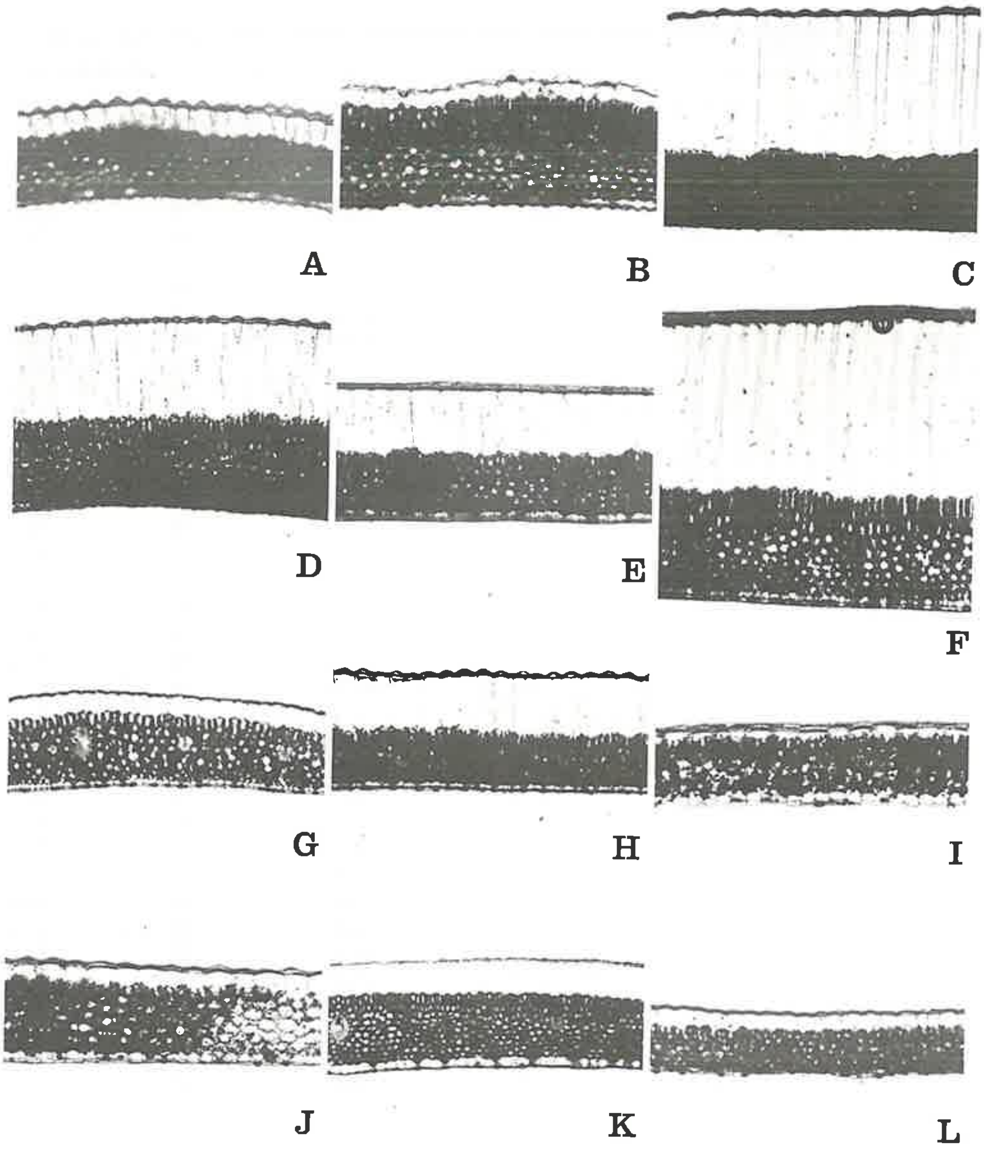

Fig. 4. Cross sections of leaves.
A, *P. delenatii.* B, *P. micranthum.* C, *P. bellatulum.* D, *P. concolor.* E, *P. randsii.* F, *P. parishii.* G, *P. insigne.* H, *P. fairrieanum.* I, *P. lawrenceanum.* J, *P. purpuratum.* K, *P. chamberlainianum.* L, *P. glaucophyllum.* × 18.

Polyantha (0.70–2.10 mm) and Paphiopedilum (0.6–1.43 mm). Differences of variation in leaf-thickness among the subgenera seem to suggest that the species of each subgenus are growing at similar habitats or at different habitats (shady or sunny).

B) Thickness of epidermis is also showing a wide variation and varies from 0.05 mm (*P. purpuratum*) to 1.27mm (*P. parishii*), and it is considered to be characteristic for these species. The thickness of epidermis is rather stable in some subgenera; e.g. 0.15–0.27mm in Parvisepalum, 0.70–1.03 mm in Brachypetalum, 0.13–0.25 mm in Cochlopetalum and 0.05–0.27 mm in Sigmatopetalum. But in subgenus Polyantha and Paphiopedilum, the thickness of epidermis is showing wide variations such as 0.11–1.27 mm in Polyantha and 0.10–0.73 mm in Paphiopedilum. On the contrary, the thickness of mesophyll is not neccessarily variable in this genus than those of epidermis; they vary from 0.40 mm (*P. fairrieanum*) to 0.77 mm (*P. elliottianum*). The anatomical features of leaf cross section indicate that the thickness of mesophyll is almost uniform throughout the genus, and the differences in leaf-thickness are apparently caused by the thickness of epidermis.

C) The upper surfaces of epidermis are almost smooth in most species, while in the species of subgenus Parvisepalum and Brachypetalum they are distinctly mamillate or conically projected and rough to touch (Fig. 5). The occurrence of leaf surface projection does not seem to be related with the other leaf characters. As in the other plants, the mamillate and thick-walled epidermis are considered to be an adapted form to rather xeric habitats. It is the useful specific character whether the epidermis surface is smooth or rough.

D) The size of stomata in *Paphiopedilum* varies from 37 μm (*P. concolor, P. villosum*) to 67 μm (*P. urbanianum*) in diameter, and the median size of stomata in *Paphiopedilum* is 51.8 μm, and the ratio (max./minim.) is 2.4. The density of stomata vary widely from 12.0/mm^2 (*P. lawrenceanum*) to 86.6/mm^2 (*P. charlesworthii*), and the maximum one is 7 times of minimum one (Table 2). As shown in Table 2 the size of stomata does not vary so much in *Paphiopedilum*.

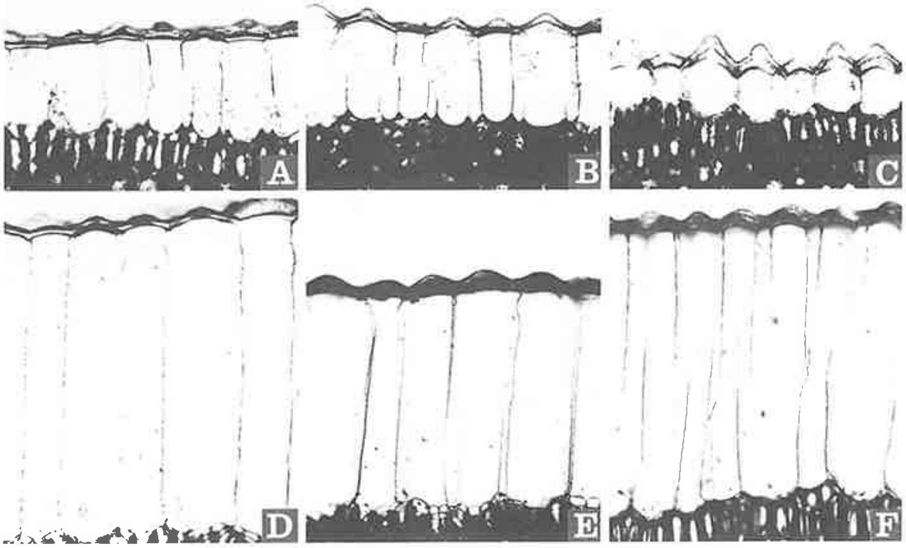

Fig. 5. The fine structure of leaf-surface and epidermis.
A, *P. armeniacum*. B, *P. delenatii*. C, *P. micranthum*. D, *P. bellatulum*. E, *P. concolor*. F, *P. niveum*. x 45.

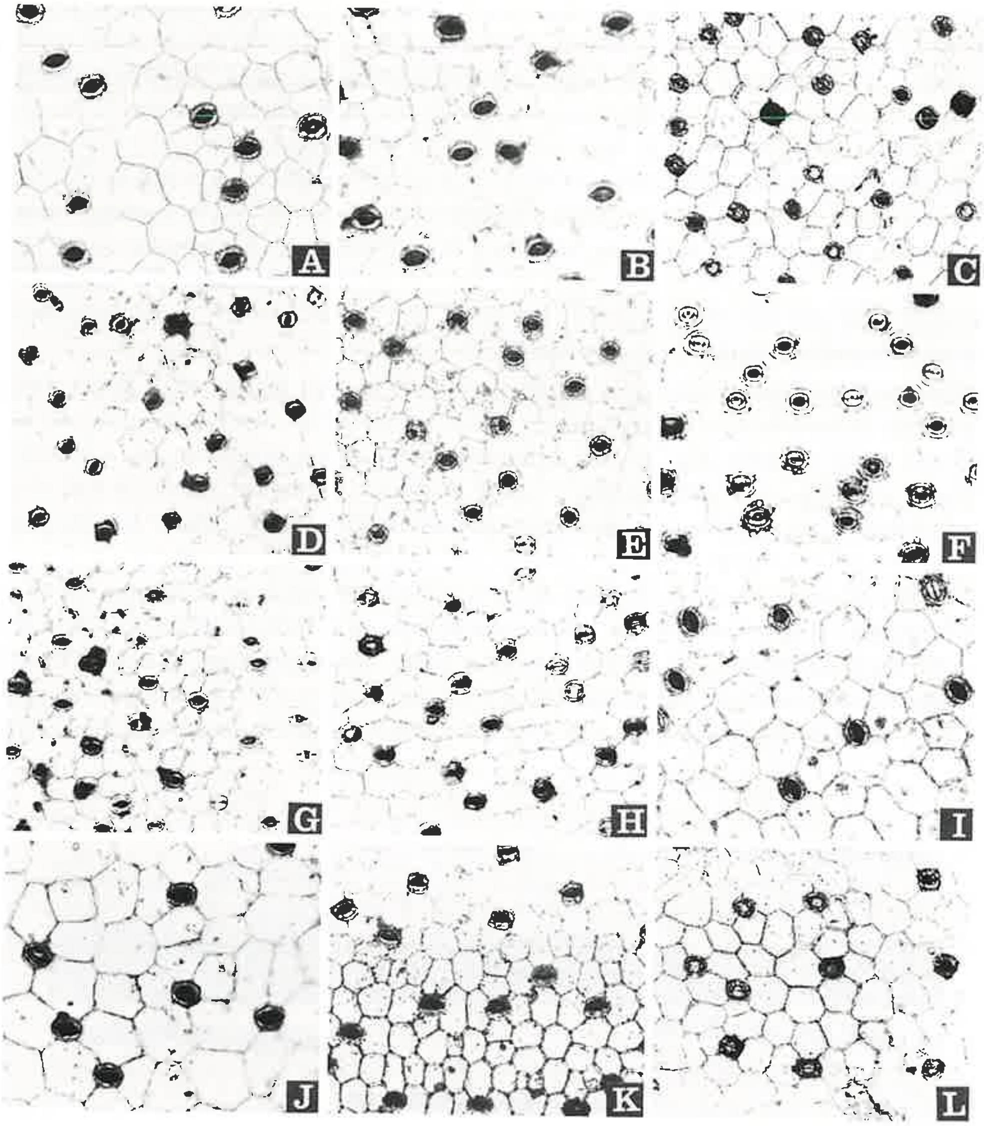

Fig. 6. Variations in size and density of stomata.
A, *P. delenatii.* B, *P. micranthum.* C, *P. bellatulum.* D, *P. concolor.* E, *P. randsii.* F, *P. parishii.* G, *P. insigne.* H, *P. fairrieanum.* I, *P. lawrenceanum.* J, *P. purpuratum.* K, *P. chamberlainianum.* L, *P. glaucophyllum.* × 60.

Though the density of stomata vary greatly within this genus, it seems to be rather uniform for most subgenera. Exceptionally, subgen. Polyantha (28–51/mm^2) and Paphiopedilum (37–87/mm^2) are exhibiting wide variations in the density of stomata. In the taxonomy of *Paphiopedilum,* it is inferable to be a noteworthy features whether the density of stomata for each taxon (mainly for subgenus) is uniform or not, and their range is narrow or wide.

In summary, it semms to be impossible to discuss about the above mentioned anatomical features of leaves which is primitive or *vice versa,* except the surface projections of epidermis. But these features provide us useful suggestions in considering the relations or differences between the taxa (mainly subgenera) and the uniformity or diversification of each taxon.

3. Inflorescence

As in the other genera of Orchidaceae, inflorescence of the genus *Paphiopedilum* is essentially a raceme type (Pfitzer 1903, Brieger 1971, etc.). The flowers of the most members of this genus are usually only one (occasionally two) at the tip of racemes (species of subgenus Parvisepalum, Brachypetalum, Paphiopedilum and Sigmatopetalum), whereas in the species of subgenus Polyantha and Cochlopetalum the racemes are always bearing 3–6, rarely 10 or more flowers on it (pluri-flowered raceme). The pluri-flowered racemes as observed in subgenus Polyantha and Cochlopetalum are classified into following two types (Fig. 7, 8): 1) the flowers of Polyantha (e.g. *P. haynaldianum, P. philippinense,* etc.) open simultaenously, and

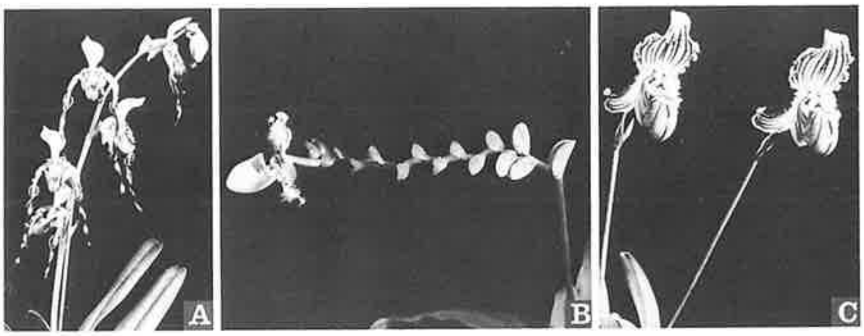

Fig. 7. Flowering modes in *Paphiopedilum.*
A, *P. parishii.* B, *P. glaucophyllum.* C, *P. fairrieanum.*

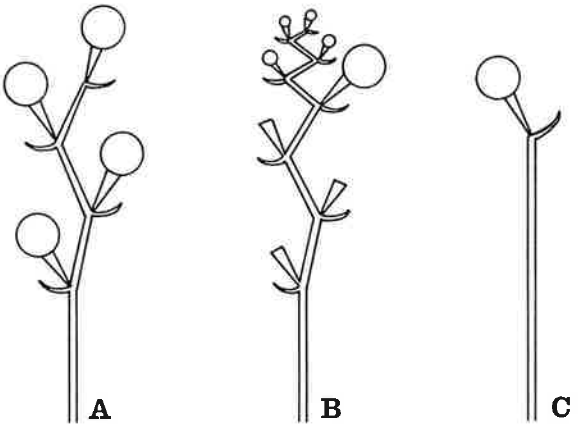

Fig. 8.
Three types of inflorescence.
A, Simultaenously spreading, pluri-flowered raceme.
B, Separately spreading, pluri-flowered raceme.
C, Uni-flowered raceme.
Large circle indicates the spreading flower.

2) the flowers of Cochlopetalum are spreading out only one and open successively from base to tip (*P. glaucophyllum, P. liemianum,* etc.). These differences in the flower number have been regarded as an important taxonomic criterion by some authors (Brieger 1971, etc.), and they had often regarded this difference as the primarily important character in the recognition of subgenus. As observed in the other genera of Orchidaceae, pluri-flowered racemes are commonly observed in the closely related genera, such as in *Phragmipedium, Selenipedium* and *Cypripedium.* In addition to the above mentioned two types, there are transitional forms in many species under different kinds of growth conditions. Usually the well developed, vigorous plants are often spreading out two-flowered racemes even in the essentially uni-flowered species. It seems to indicate that tentative occurrence of two-flowered racemes is an indication of essential flowering mode. Thus in the *Paphiopedilum,* the pluri-flowered racemes seem to be a primitive character, and the uni-flowered racemes is a derived one from the former.

4. Floral characters

1) Perianth

As in the other genera, perianth of *Paphiopedilum* are specialized into following 5 parts: they are dorsal and lower sepals, two lateral petals and lip. Lower sepal is, as indicated by many authors (Pfitzer 1903, Brieger 1971, etc.), a connate one deriving from the connection of lower lateral two sepals which are commonly observed in genera of the other subfamilies. In *Paphiopedilum,* the various kinds of variations of these perianth are providing us useful taxonomic characters, and the variations of each parts are fully discussed in the following parts. Before the detailed discussions of each part, we have to remember that these 5 parts are same in origin and have specialized into 5 different parts along with the evolution of this genus (Brieger 1971).

In this subfamily, lip is much differentiated from the rest ones in its shape and other characters. The petals and sepals in the genera of the other subfamilies are more or less similar not only in the shape but also in coloring. This seems to suggest that the flower of which petals and sepals are similar in shape, size and coloring is relatively primitive.

There is nothing to say that the shape of lip is quite different from the rest perianth, and the nature and coloring are very variable within this genus. The lips in the species of subgen. Parvisepalum and Brachypetalum are sharing common features in coloring and nature with those of the rest perianth. While the lips in the species of subgenus Polyantha, Paphiopedilum and Sigmatopetalum are entirely different in coloring. Considering the origin of lip, the lip of which coloring is common with that of petals and sepals is inferable as the most primitive.

A) Sepals

As in the other genera of Cypripedioideae, there are two sepals in the flower, namely the upper and lower (synsepal) sepals, while the flowers of the other genera of Orchidaceae naturally have three sepals, namely one upper sepal and two lateral sepals. The detailed morphology of upper sepal is more variable than in the other genera, and is one of the important characteristics for each species.

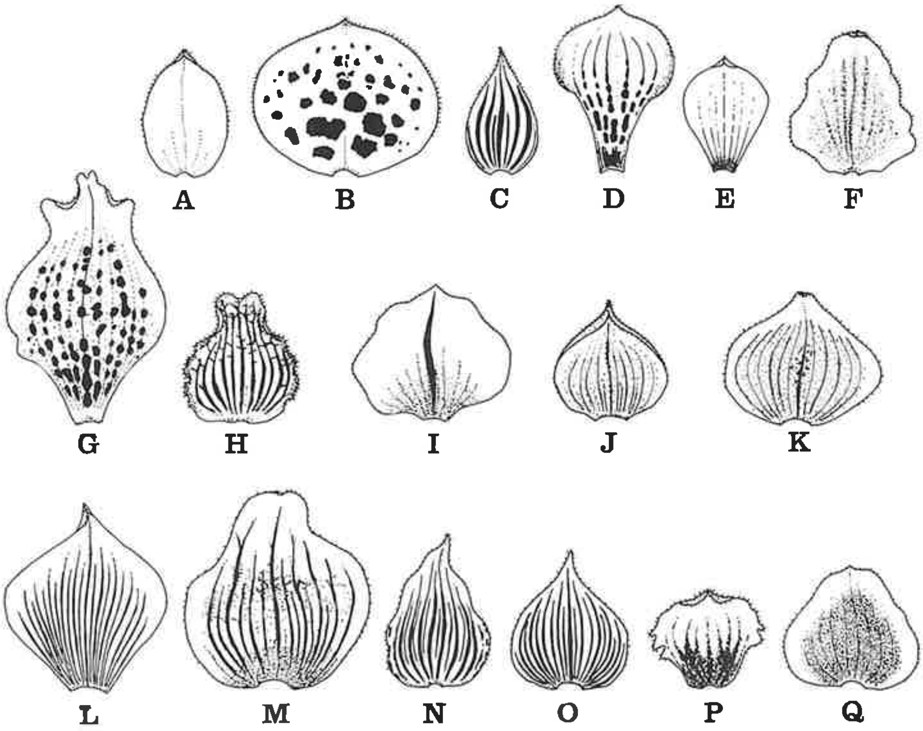

Fig. 9. Shapes and markings of upper sepals.
A, *P. delenatii*. B, *P. bellatulum*. C, *P. randsii*. D, *P. haynaldianum*. E, *P. parishii*. F, *P. hirsutissimum*. G, *P. insigne*. H, *P. fairrieanum*. I, *P. spicerianum*. J, *P. hookerae*. K, *P. mastersianum*. L, *P. tonsum*. M, *P. lawrenceanum*. N, *P. argus*. O, *P. venustum*. P, *P. chamberlainianum*. Q, *P. liemianum*. × 0.5.

The shapes of upper sepal are elliptic (or broad elliptic), ovate (or broad ovate) or obovate (broad obovate), and they are characteristic for each species (Fig. 9). In most species of *Paphiopedilum,* upper sepal is much larger than lower one, but it is sometimes almost same in size (*P. stonei, P. philippinense, P. rothschildianum,* etc.) or exceptionally smaller (*P. delenatii, P. armeniacum, P. micranthum*). The relative size of upper sepal with lower one seems to be characteristic for some species assemblages. Though there are many transitional forms in surface color pattern of upper sepal, they are classified into following three types: 1) almost monotone throughout (*P. delenatii, P. armeniacum*), 2) speckeled (spotted) with many small spots (*P. bellatulum, P. concolor,* etc.), and 3) vertically striped (*P. dayanum, P. rothschildianum, P. fairrieanum, P. purpuratum,* etc.). These kinds of surface color patterns are characteristic for some subgenera, but in subgenus Paphiopedilum there are different kinds of surface patterns and many transitional forms between them.

As in the other genera of Cypripedioideae, the lower sepal in *Paphiopedilum* is a connate one deriving from the fusion of lateral two sepals, which are naturally separated in most genera of Orchidaceae. The lower sepal in some species is well developed and serves us useful characteristic for identifying the species (*P. rothschildianum, P. philippinense,* etc.), but the lower sepals in most species are not different species by species in most subgenera.

B) Petals

The shape, size, color pattern and hairiness of petals are much differentiated than those of sepals, and those differences have often been employed in classifying or distinguishing the species or species assemblages (Fig. 10). The shapes of petals are roughly classified into following 5 main types: 1) broad ovate (*P. bellatulum, P. delanatii,* etc.), 2) oblong to elliptic (*P. sukhakulii, P. purpuratum,* etc.), 3) spathulate (*P. lowii, P. haynaldianum,* etc.), 5) ensiform with distortion (*P. parishii, P. philippinense,* etc.), but there are many transtional shapes between them. It is not to speak of that shapes of petal are significant character, and they seem to be rather uniform for each subgenus or section.

There are also many surface color patterns in *Paphiopedilum,* and they are roughly classified into following 4 main types: 1) non figured and monotone petals (*P. delenatii, P. armenia-*

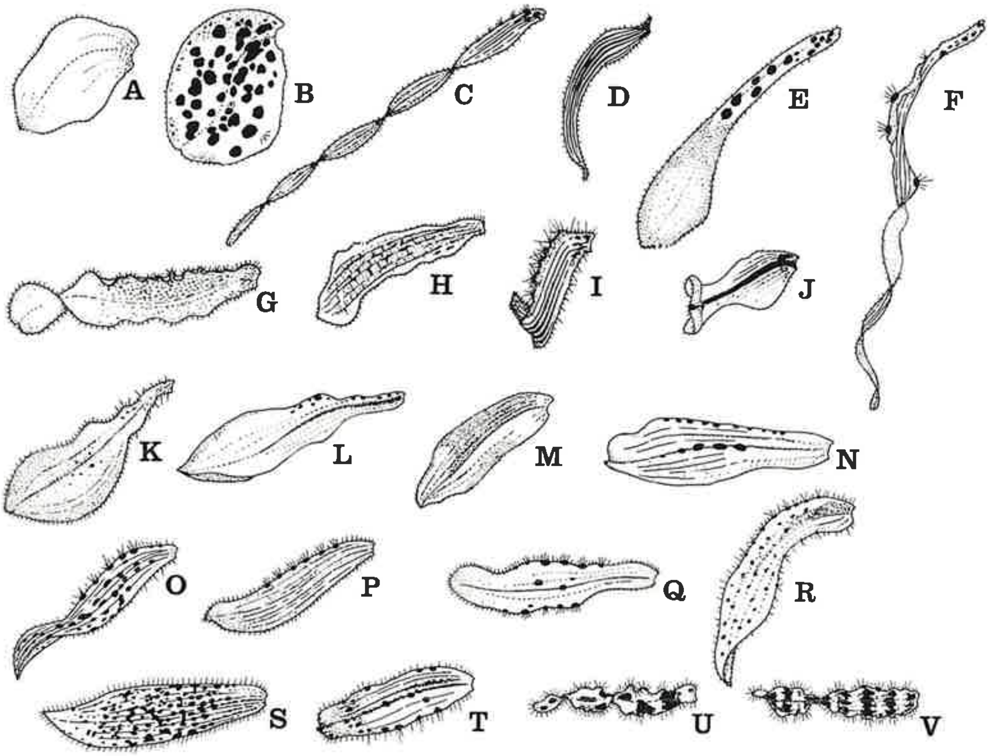

Fig. 10. Shapes and markings of petals.
A, *P. delenatii.* B, *P. bellatulum.* C, *P. philippinense.* D, *P. randsii.* E, *P. lowii.* F, *P. parishii.* G, *P. hirsutissimum.* H, *P. insigne.* I, *P. fairrieanum.* J, *P. druryi.* K, *P. hookerae.* L, *P. appletonianum.* M, *P. violascens.* N, *P. tonsum.* O, *P. argus.* P, *P. barbatum.* Q, *P. lawrenceanum.* R, *P. superbiens.* S, *P. sukhakulii.* T, *P. venustum.* U, *P. chamberlainianum.* V, *P. liemianum.* x 0.5.

cum, etc.), 2) rather regularly speckled with more or less small spots (*P. bellatulum, P. concolor, P. ciliolare,* etc.), 3) irregularly speckled with large spots or tessellated (*P. glaucophyllum, P. chamberlainianum,* etc.), 4) speckled at marginal portion with large, warty and ciliate spots (*P. barbatum, P. callosum,* etc.). The types of surface color pattern are, of course, good taxonomic criteria for the classification of *Paphiopedilum.*

In some species of *Paphiopedilum,* there are fine, short cilia on marginal portion of petals (*P. dayanum, P. purpuratum, P. sukhakulii,* etc.), while the hairs (cilia) are bearing only from the deep purple, warty spots (*P. argus, P. barbatum, P. callosum,* etc.). The occurrence or the absence of the cilia and the distribution of cilia are also good characteristics in recognizing species and some species assemblages.

C) Lip

As in the other genera of Cypripedioideae, the mid-lobe of lip is forming a pouch and those of lateral lobes are incurving into spurious claw, though they vary greatly in size and shape. In regard to the detaild morphology of pouch, following variations are observed in *Paphiopedilum* (Fig. 11): 1) calceolate pouch having no auricle and of those margin distinctly incurving at mouth (*P. delenatii, P. armeniacum* and *P. micranthum*), 2) ovoid pouch having no auricle and of those margin clearly incurving at mouth (*P. bellatulum, P. concolor,* etc.), 3) helmet-shaped pouch having no auricle and of those margin only slightly incurving at mouth (*P. rothschildianum, P. stonei, P. philippinense,* etc.) and 4) pot-shaped pouch with faint constriction at middle or just below mouth and having distinct bi-auricles at both sides of mouth, and those margin more or less recurved (*P. chamberlainianum, P. barbatum, P. appletonianum, P. villosum,* etc.). Most species of *Paphiopedilum* are belonging to above mentioned 4 types, and species in same subgenus have the same type pouch. But there are two exceptional species, namely *P. randsii* and *P. elliottianum.* The pouch of *P. randsii* has distinct bi-auricles and those margins are incurving at mouth. The pouch of *P. elliottianum,* on the contary, has no auricle and the margin is somewhat recurving. Addition to the above mentioned morphological differences: pouch of type 1) is thin, glassy and wrinkled; pouch of type 3) and 4) are more or less fleshy, waxy and not wrinkled; and pouch of type 2) exhibits intermediate features between the two extremes. Thus the morphological characters of lips in *Paphiopedilum* are linking to each other and show very wide variations, but there are many transitional types between the extremes. Within subgenus Polyantha, the lips are beautifully arranged in a line based on the detailed differences (see Table 5). Similar differentiation series of lip is also observed in the genus *Phragmipedium*: 1) lip calceolate, margin strongly incurved, ear not developed (*P. schlimii*), 2) lip oval to pot-shaped, margin faintly incurved, ear not developed (*P. sargentianum, P. caudatum,* etc.), 3) lip pot-shape, margin almost straight, ear well developed (*P. hartwegii, P. boisserianum,* etc.). Associating with the differentiation series of lip, the nature of lip in *Phragmipedium* is also changing from glassy and wrinkled to relatively thick and waxy ones. Thus the morphological features of lips in *Paphiopedilum* and *Phragmipedium* are considerd to have evolved in parallel.

Surface color pattern of lip is very variable. Those of some taxa (subgen. Parvisepalum and Brachypetalum) are not different from those of petals and sepals (type 1), while the lip of rest taxa are entirely different from those of petals and sepals (type 2). As discussed before, the same origin of the lip with other perianth seems to suggest that lip Type 1 is a primitive feature and Type 2 as derived one.

2) Stigmata

As figured by Brieger (1971), the stigmata in most species of *Paphiopedilum* are well characterized by a thick and short stalk with a much swollen, rounded tip, and surface of stigmata is somewhat widened and shallowly furrowed by three grooves. The stigmata of *P. delanatii,* exceptionally, are distinctly different from those of the other species and are well characterized by the long and very thick stalk, and somewhat spoon-shaped tips. The surface furrows of stigmata in *P. delenatii* are much deeper than those of others. As shown in Fig. 12 & 13, the

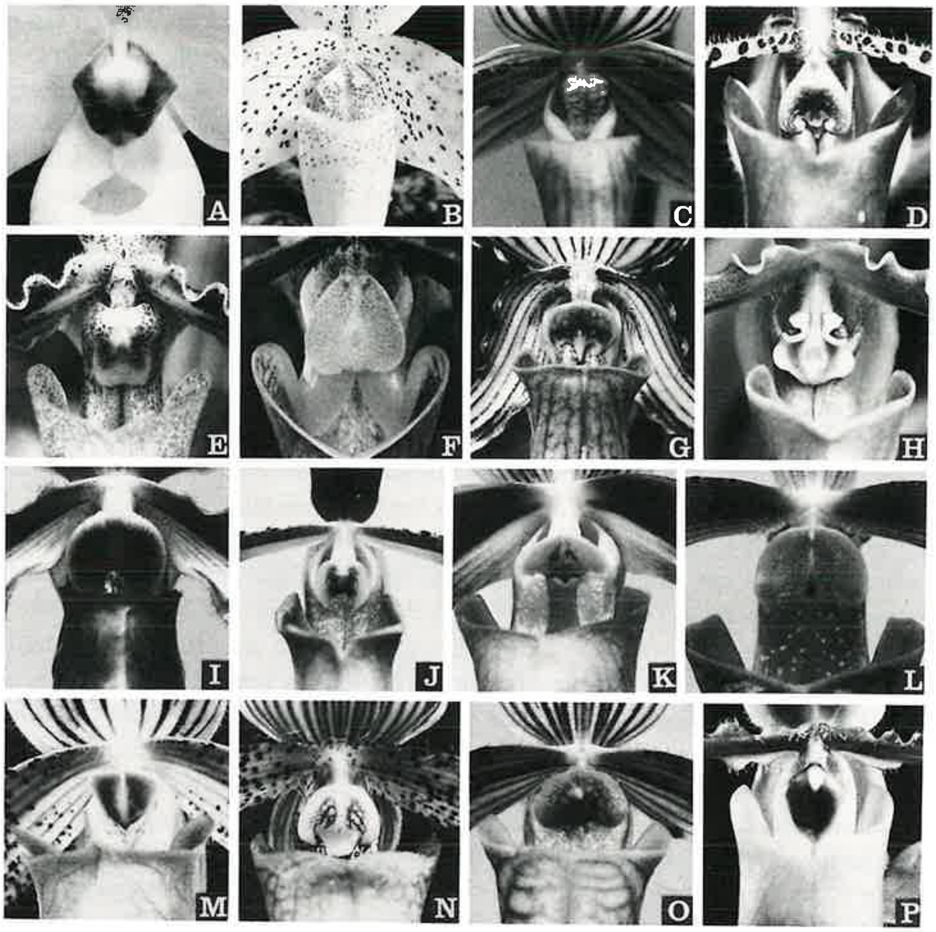

Fig. 11. Variations of lip-mouth and staminode.
A, *P. delenatii.* B, *P. concolor.* C, *P. philippinense.* D, *P. lowii.* E, *P. hirsutissimum.* F, *P. insigne.* G, *P. fairrieanum.* H, *P. spicerianum.* I, *P. hookerae.* J, *P. appletonianum.* K, *P. violascens.* L, *P. tonsum.* M, *P. acmodontum.* N, *P. sukhakulii.* O, *P. venustum.* P, *P. victoria-regina.* × 1.

stigmata of *P. delenatii* are also different from others in its position to staminode: stigmata are located just behind staminode, and apical spoon-shaped parts are almost straightly bending downwards. The stigmata of the other species are more or less bending with an angle, and the tip of stigmata is slightly apart from staminode. The detailed characters of stigmata of *P. delenatii* are very similar to those of *Cypripedium* species. Though we are regrettably could not examine the stigmata of *P. armeniacum* and *P. micranthum*, the figures illustrated by Chen & Liu (1982) show that the stigmata of *P. armeniacum* are just the same type with that of *P. delenatii*: stalk and tip of stigmata are almost straight and locating just behind the staminode. With regard to the stigmata, *P. armeniacum* and *P. delenatii*, probably and *P. micranthum*, are rather closely related to those of *Cypripedium* than to those of the rest species of *Paphiopedilum*.

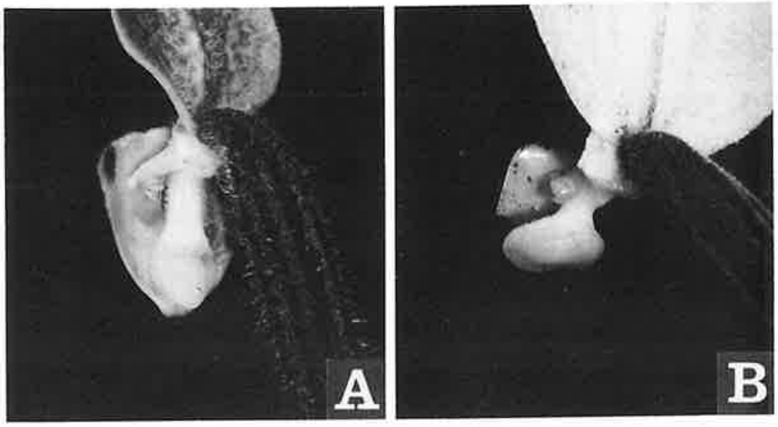

Fig. 12.
Comparison of two types of column.
A, *P. delenatii*. B, *P. concolor*.

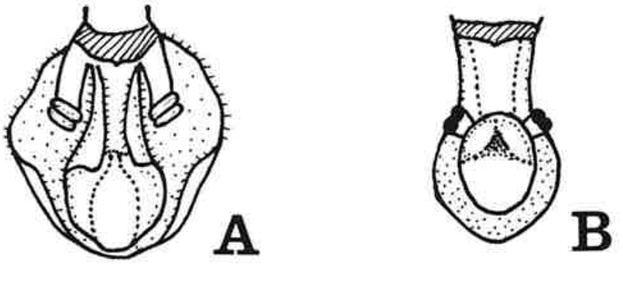

Fig. 13.
Ventral views of two types of column.
A, *P. delenatii*. B, *P. bellatulum*. x 2.

3) Pollinia

The pollinia of *Paphiopedilum* have been considered to be all viscous, and there has never been made any extensive observation on pollinia in this genus. Close examination of pollinia revealed that the pollinia of *P. delenatii* are granulous. Chen & Liu (1981) did not describe whether the pollinia are granuous or viscous in their original description of *P. armeniacum*. The long stalk of anther and long column seems to suggest the probability of the pollinia of *P. armeniacum* being granulous.

The pollinia of the species of *Cypripedium* have been considered to be unexceptionally granulous. But during the course of this study, we found that the pollinia of *Cypripedium macranthum* are apparently viscous. In addition, the detailed morphology of anther in *C. macranthum* is very similar to those of *Paphiopedilum* having viscous pollinia. It is noteworthy that there are similar differentiation series of pollinia in both genera, such as *Cypripedium* and *Paphiopedilum,* for the recognition of phylogenetic tendencies in subfamily Cypripedioideae. Although the viscous pollinia and solid-mass pollinia are common in Orchidaceae, the pollen grains in Spermatophyta are generally granulous. It is generally inferable that the granulous pollinia are primitive and the viscous ones are derived.

4) Staminode

Though there are some intraspecific variations in shape and size (Fig. 11, 15), the morphology of staminode in *Paphiopedilum* has long been considered to be the primarily important characteristics in classification (Pfitzer 1903, Brieger 1971). The morphological variations of staminode are providing us the important criteria of various ranks of taxa. In some subgenera and sections, differentiations of staminode are useful specific characters (Fig. 14). For example, the staminode variation in subgenus Polyantha is as follows: 1) broad-ovate to transversely broad-ovate with a blunt or tridentate tip in *P. haynaldianum*; 2) elliptic to ovate with dense, brownish hairs at margin in *P. stonei* and *P. philippinense*; 3) narrow elliptic, rostrate and bending downward with an acute angle with dense, brownish hairs on whole surface in *P. rothschildianum*; 4) narrow elliptic, rostrate and bending upward with an acute angle, with dense, brownish hairs on surface in *P. elliottianum.* On the other hand, the morphological characters of staminode are almost uniform in some subgenera or sections: rhombic elliptical, with hairs at basal portion in subgenus Cochlopetalum; ovate (3:2–6:5), faintly tridentate at lower tip, and with a small protuberance at middle in sect. Paphiopedilum: lunate, smooth and almost plain in subsect. Barbata: semi-circular, smooth and plain in subsect. Loripetalum.

There are two types of surface coloring of staminode. Surface of staminode in subgen. Parvisepalum and Brachypetalum are showing same pattern (coloring) with those of perianth (Type 1). The surface of staminode in the rest taxa are different from those of perianth (Type 2). Common surface coloring of staminode is also considered to be a primitive feature as discussed in lip (see p. 15).

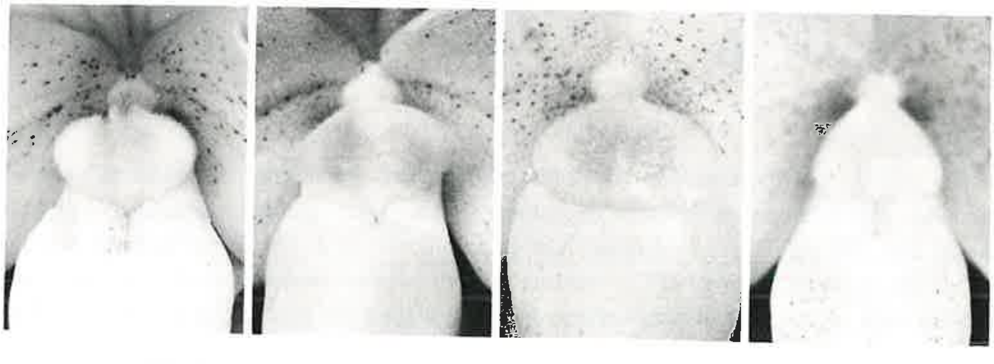

Fig. 14. Intraspecific variation of staminode in *P. niveum.* x 1.6.

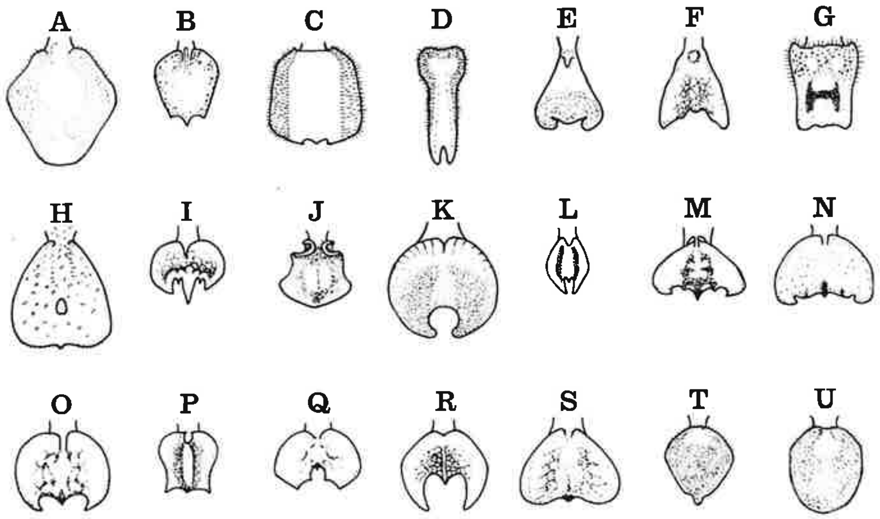

Fig. 15. Shapes of staminode.
A, *P. delenatii.* B, *P. bellatulum.* C, *P. praestans.* D, *P. rothschildianum.* E, *P. lowii.* F, *P. parishii.* G, *P. hirsutissimum.* H, *P. insigne.* I, *P. fairrieanum.* J, *P. spicerianum.* K, *P. hookerae.* L, *P. bullenianum.* M, *P. violascens.* N, *P. tonsum.* O, *P. barbatum.* P, *P. acmodontum.* Q, *P. virens.* R, *P. sukhakulii.* S, *P. venustum.* T, *P. chamberlainianum.* U, *P. liemianum.* x 1.

5. Seeds

Two extreme forms of seeds are observed in the genus (Fig. 16). The seeds of the species of subgenus Brachypetalum, Polyantha (except *P. rothschildianum*) and Paphiopedilum are almost oval and 0.5 – 0.6 mm long. The seeds of the subgenus Sigmatopetalum are much longer (about 1.5 mm long) and thread-like. The seeds observed in subgenus Cochlopetalum and some species (*P. delenatii, P. rothschildianum,* etc.) are the intermediate in shape and size between the two extremes. Though there are wide variations of seeds in shape and size, the size of embryo is not different even in the seeds of two extremes, and they are always 0.3– 0.4 mm long in size (Table 3). Those conditions of seeds suggest that the seed observed in subgenus Sigmatopetalum has a larger epidermal cell which is inflated by much air within it. Comparing with the relatively rounded seeds, the thread-like seeds seem to be more convenience for the long dispersal. Actually the taxa which produce large seeds have, in most cases, a wide distributional range (see Fig. 24)

6. Hairs

In *Paphiopedilum,* various kinds of hairs are observed on plant surface, especially they are much frequently observed on the floral parts. The surfaces of scapes are always covered with short, very thin hairs throughout. There are two types of hairs are observed on perianth

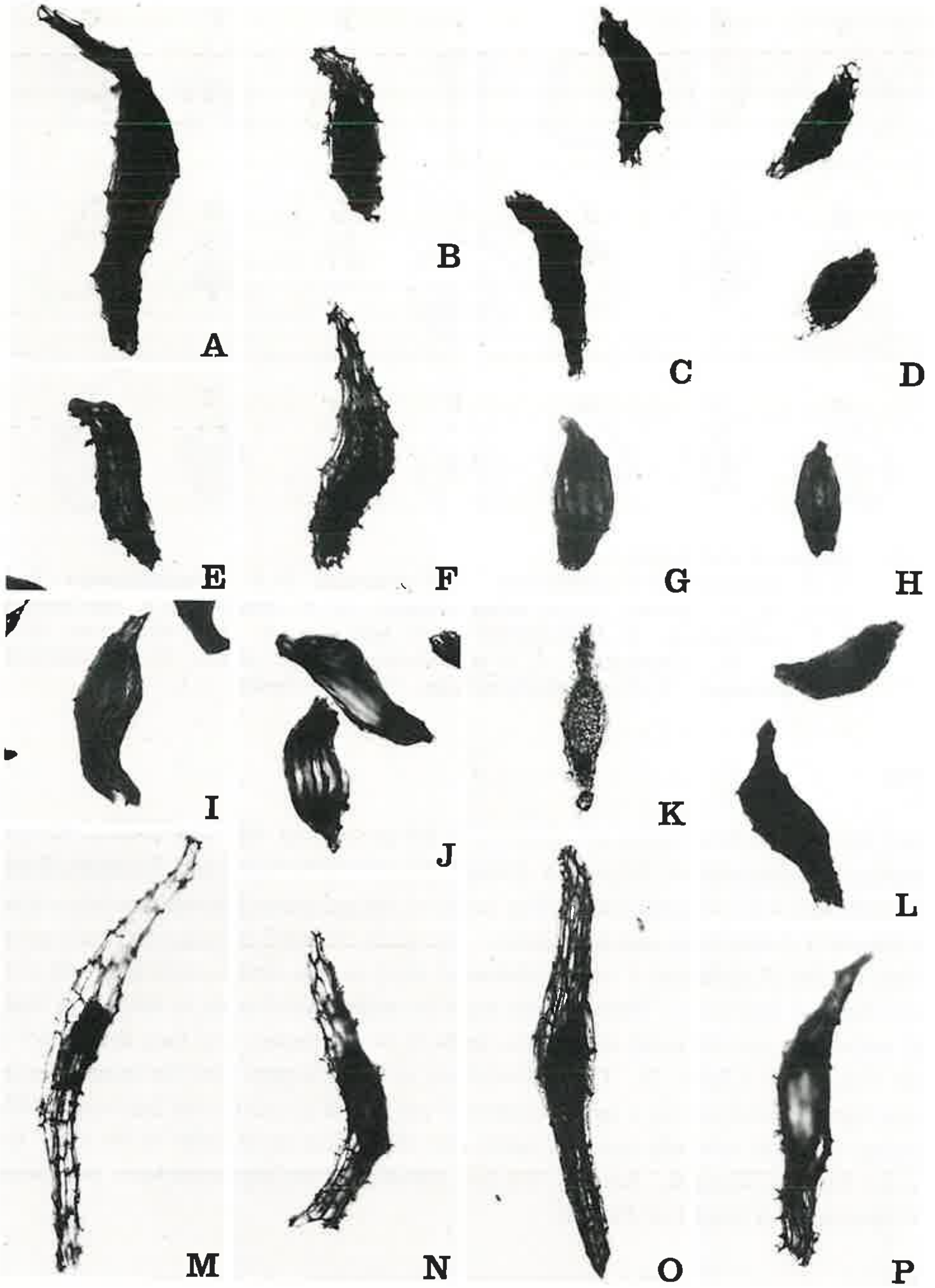

Fig. 16. Variation of seeds.
A, *P. delenatii.* B, *P. bellatulum.* C, *P. concolor.* D, *P. godefroyae.* E, *P. philippinense.* F, *P. rothschildianum.* G, *P. haynaldianum.* H, *P. lowii.* I, *P. hirsutissimum.* J, *P. insigne.* K, *P. fairrieanum.* L, *P. druryi.* M, *P. ciliolare.* N, *P. acmodontum.* O, *P. venustum.* P, *P. liemianum* var. *primulinum.* × 45.

Table 3. Size of seeds and embryo.

Species	Seed		Embryo	
	Length (mm)	Width (mm)	Length (mm)	Width (mm)
delenatii	1.00	0.18	0.23	0.13
bellatulum	0.43	0.15	0.24	0.13
concolor	0.50	0.13	0.24	0.12
godefroyae	0.35	0.15	0.21	0.12
philippinense	0.51	0.14	0.25	0.14
rothschildianum	0.81	0.15	0.25	0.13
stonei	0.92	0.17	0.22	0.12
haynaldianum	0.44	0.17	0.23	0.12
lowii	0.34	0.12	0.20	0.10
hirsutissimum	0.58	0.16	0.29	0.13
insigne	0.48	0.17	0.30	0.13
fairrieanum	0.51	0.17	0.21	0.13
druryi	0.66	0.15	0.26	0.13
callosum	1.09	0.15	0.21	0.10
ciliolare	1.16	0.13	0.24	0.11
acmodontum	0.79	0.15	0.23	0.11
purpuratum	1.12	0.12	0.22	0.11
venustum	1.01	0.14	0.24	0.12
glaucophyllum	0.74	0.20	0.24	0.14
liemianum var. *primulinum*	0.67	0.17	0.30	0.11

surface. First type of hairs is long and well recognizable by naked eyes, and they are usually tinged with deep blackish purple or deep brown. Another type of hairs is very short and hardly recognizable by naked eyes, and is tinged with paler color. The first type of hairs is classified into two subtypes by the differences in the localizations: hairs of subtype 1) are spreading out from the large, warty spots which are locating at the marginal portion of lateral petals (e.g. *P. callosum, P. argus,* etc.), and hairs of subtype 2) are spreading out from the bare marginal portion of lateral petals (e.g. *P. dayanum, P. ciliolare,* etc.). The hairs of subtype 1) are always restricted to the warty parts and the rest margin of lateral petals is almost naked. While the hairs of subtype 2) are regularly and uniformly scattered throughout the margin of petals. The difference between the subtype 1) and 2) is often very useful for distinguishing the closely related species assemblages, as in the recognition of sections in subgenus Sigmatopetalum.

The leaves in the most species of *Paphiopedilum* are naked throughout, but there are long, almost hyaline hairs on marginal portion of leaves in subgenus Cochlopetalum: there are long, hyaline hairs on the whole margin of leaves in *P. liemianum,* while the hairs limited to the basal portion of leaves in the rest species.

Thus the presence or absence of hairs at various parts of plants and those lengh and color are serving us important taxonomic criteria in recognizing the various ranks of taxa.

7. Chromosomes

Since Mehlquist (1947) many observations have been made on the chromosomes of this genus (Duncan & MacLeod 1947, 1948, 1949, 1950, Kamemoto *et al.* 1963, Tanaka & Aoyama 1974, Karasawa 1979, etc.). The extensive observations and discussions on chromosomes of *Paphiopedilum* have been made by Karasawa (1978, 1979, 1980, 1982.), and he reported chromosome numbers and their karyotypes of 70 taxa of this genus. *Paphiopedilum* is, at the present time, one of the well studied genera in Orchidaceae (Table 4). According to Karasawa (1979), the number and the detailed morphology of chromosomes are not only characteristic

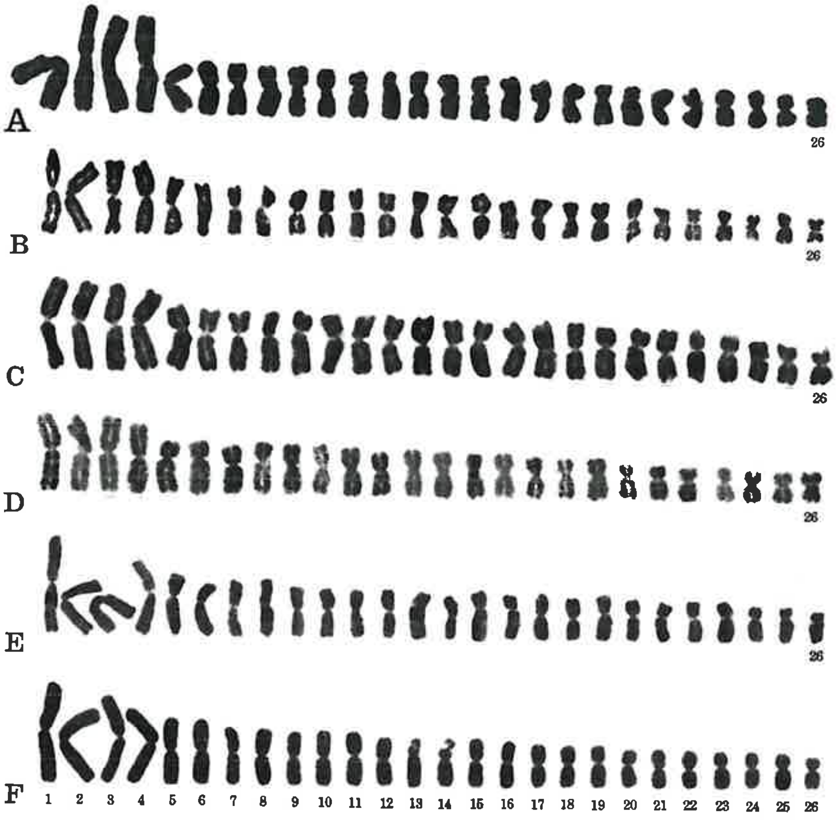

Fig. 17. Karyotype variations of the 2n=26 species.
A, *P. micranthum.* B, *P. bellatulum.* C, *P. philippinense.* D, *P. lowii.* E, *P. insigne.* F, *P. fairrieanum.* x 1000.

Table 4. Chromosome numbers of the species of *Paphiopedilum*.

Species	Chromosome number (2n)	References
armeniacum	26	Chen & Liu 1982.
	26=26V	Karasawa 1982.
delenatii	26	Mehlquist 1947, Duncan 1947, Duncan & MacLeod 1948.
	26=26V	Karasawa 1979.
micranthum	26=26V	Karasawa 1982.
bellatulum	26	Mehlquist 1947, Duncan 1947, Duncan & MacLeod 1948, Kamemoto *et al.* 1963.
	26=26V	Karasawa 1979.
concolor	26	Duncan & MacLeod 1948, Kamemoto *et al.* 1963.
	26=26V	Karasawa 1979.
leucochilum	26=26V	Karasawa 1979.
niveum	26	Mehlquist 1947, Duncan 1947, Duncan & MacLeod 1948, Kamemoto *et al.* 1963.
	26=26V	Karasawa 1979.
elliottianum	26=26V	Karasawa & Aoyama 1980.
philippinense	26	Duncan & MacLeod 1949, Pancho 1965, Tanaka & Aoyama 1974.
	26=26V	Karasawa 1979.
praestans	28	Duncan & MacLeod 1948.
	26=26V	Karasawa 1979.
randsii	26=26V	Karasawa 1979.
rothschildianum	26	Duncan 1947.
	28	Duncan & MacLeod 1949.
	26=26V	Karasawa 1979.
stonei	26	Duncan 1947, Duncan & MacLeod 1949.
	26=26V	Karasawa 1979.
haynaldianum	26	Duncan 1947, Duncan & MacLeod 1949, Pancho 1965, Tanaka & Aoyama 1974.
	26=26V	Karasawa 1979.
lowii	26	Duncan 1947, Duncan & MacLeod 1949, Tanaka & Aoyama 1974.
	26=26V	Karasawa 1979.
parishii	26	Duncan 1947, Duncan & MacLeod 1949, Kamemoto *et al.* 1963.
	26=26V	Karasawa 1979.

Table 4. (continued)

hirsutissimum	26	Duncan 1947, Duncan & MacLeod 1949, Sasa & Torigata 1967, Tanaka & Aoyama 1974.
	26=26V	Karasawa 1979.
charlesworthii	26	Duncan 1947, Duncan & MacLeod 1949.
	26=26V	Karasawa 1979.
exul	26	Duncan 1947, Duncan & MacLeod 1949, Kamemoto *et al.* 1963, Tanaka & Aoyama 1974.
	26=26V	Karasawa 1979.
insigne	26	Mehlquist 1947, Duncan 1947, Duncan & MacLeod 1948, Tanaka 1965, Sasa & Torigata 1967, Tanaka & Aoyama 1974.
	26=26V	Karasawa 1979.
villosum	26	Mehlquist 1947, Duncan 1947, Duncan & MacLeod 1948, Kamemoto *et al.* 1963.
	26=26V	Karasawa1979.
fairrieanum	26	Mehlquist 1947, Duncan 1947, Duncan & MacLeod 1949, Tanaka & Aoyama 1974.
	26=26V	Karasawa 1979.
druryi	26	Duncan 1947, Duncan & MacLeod 1949.
	30=22V+8I=26V	Karasawa 1979.
spicerianum	28	Duncan & MacLeod 1949.
	30	Francini 1930, 1931, 1932, Tanaka & Aoyama 1974.
	30=22V+8I=26V	Karasawa 1979.
hookerae	28=28V	Karasawa 1979.
appletonianum	38=14V+24I=26V	Karasawa 1979.
bullenianum	40=12V+28I=26V	Karasawa 1979.
celebesensis	42=10V+32I=26V	Karasawa 1979.
bougainvilleanum	40=12V+28I=26V	Karasawa 1979.
mastersianum	32	Duncan 1947, Duncan & MacLeod 1950.
	36=16V+20I=26V	Karasawa 1979.
violascens	38=14V+24I=26V	Karasawa 1979.
wentworthianum	40=12V+28I=26V	Karasawa 1979.
argus	26	Pancho 1965.
	38	Tanaka & Aoyama 1974.
	38=14V+24I=26V	Karasawa 1979.
tonsum		Duncan 1947, Duncan & MacLeod 1950
	32=20V+12I=26V	Karasawa 1979

Table 4. (continued)

barbatum	38	Francini 1934, Mehlquist 1947, Duncan 1947, Duncan & MacLeod 1950.
	38=14V+24I=26V	Karasawa 1979.
callosum	32	Mehlquist 1947, Duncan 1947, Duncan & MacLeod 1950, Kamemoto *et al.* 1963, Tanaka 1965, Tanaka & Aoyama 1974
	32=20V+12I=26V	Karasawa 1979.
hennisianum	36=18V+18I	Karasawa 1979.
lawrenceanum	36	Mehlquist 1947, McQuade 1949, Duncan & MacLeod 1950.
	36=16V+20I=26V	Karasawa 1979.
ciliolare	32=20V+12I=26V	Karasawa 1979.
curtisii	36=16V+20I=26V	Karasawa 1979.
dayanum	34	Duncan 1947, Duncan & MacLeod 1950.
curtisii	36	Mehlquist 1947, Duncan & MacLeod 1950
	36=16V+10I=26V	Karasawa 1979
	36=16V+20I=26V	Karasawa 1979.
superbiens	38	Duncan 1947, Duncan & MacLeod 1950.
	38=14V+24I=26V	Karasawa 1979.
acmodontum	36=16V+20I=26V	Karasawa 1979.
javanicum	36	Duncan 1947, Duncan & MacLeod 1950.
	38=14V+24I=26V	Karasawa 1979.
urbanianum	40=12V+28I=26V	Karasawa 1982.
virens	40=12V+28I=26V	Karasawa 1979.
purpuratum	40=12V+28I=26V	Karasawa 1979.
sukhakulii	40	Senghas & schoser 1965.
	40=12V+28I=26V	Karasawa 1979.
venustum	40, 41	Tanaka & Aoyama 1974.
	42	Duncan 1947, Duncan & MacLeod 1950.
	40=12V+28I=26V	Karasawa 1979.
	41	Karasawa 1979.
chamberlainianum	32	Hoffman 1929, 1930, Duncan 1947, Duncan & MacLeod 1949.
	34=16V+18I=25V	Karasawa 1979.
glaucophyllum	36	Duncan 1947, Duncan & MacLeod 1949.
	36=14V+22I=25V	Karasawa 1979.
	37=13V+24I=25V	Karasawa 1979.
glaucophyllum var. *moquetteanum*	34=16V+18I=25V	Karasawa 1979
liemianum	32	Wood 1976.
	32=18V+14I=25V	Karasawa 1979.
victoria-regina	30=20V+10I=25V	Karasawa & Aoyama 1980.

for each species but also for subgenera and sections. The morphology of the chromosomes is well characterized by the number, size, position of centromere, presence and size of satellite, and the presence or absence of small constriction.

Chromosome numbers are generally good characteristics for each species and do not exhibit variations within a species (except in *P. ciliolare-superbiens* species complex, and *P. chamberlainianum-glaucophyllum* species complex). On the other hand, the karyotypes are exhibiting great variations even in same chromosome number by the differences in the length and position of centromere of each comprising chromosomes (Fig. 17). Karasawa (1979), based on his extensive observations, also stressed on the karyotype evolution within the genus *Paphiopedilum* that it has probably been taken out through the shifting of position of centromere, as median → submedian → subterminal.

The chromosome number in *Paphiopedilum* varies from 2n=26 to 2n=42 (Mehlquist 1947, Duncan 1947, Duncan & MacLeod 1948, 1949, 1950, Kamcmoto *et al.* 1963, Tanaka & Aoyama 1974 Karasawa 1979, etc.). The species of which chromosome number is 2n=26 are almost half number of species in this genus (22 species), and they exhibit bimodal karyotypes; namely they are comprising 4 large chromosomes (19–14 μm), and gradually shortened 22 small chromosomes. The position of centromere in 2n=26 species is usually median, but in some species it is not necessarily median; i.e., *P. randsii* has 4 submedian chromosomes, and *P. parishii* has 6 submedian chromosomes. In the species of sect. Paphiopedilum and some species of subgenus Brachypetalum, there are distinct satellite in a pair of chromosomes.

The 2n=28 species (*P. hookerae*) is showing peculiar karyotype, and it is comprising 26 metacentic chromosomes and a pair of subterminal ones.

In the relation to increasing of the chromosome numbers, the species with 2n=30–42 chromosomes show a distinct correlation between the decreasing of metacentric ones and the increasing of the telocentric ones: it is considered that the centric fission of a pair of metacentric chromosomes bears 4 telocentric ones. Every two telocentric chromosomes are converting into one metacentric chromosome, and the species with chromosome number 2n=30–42 are clearly classified into following two basic karyotypes.

The first type karyotype is appreciated 2n=26V; for example (Fig. 18)

P. spicerianum	2n = 30 = 22V + 8I = 26V
P. callosum	2n = 32 = 20V + 12I = 26V
P. acmodontum	2n = 36 = 16V + 20I = 26V
P. javanicum	2n = 38 = 14V + 24I = 26V
P. sukhakulii	2n = 40 = 12V + 28I = 26V
P. celebesensis	2n = 42 = 10V + 32I = 26V

The second type karyotype is appreciated 2n=25V; for example (Fig. 19)

P. victoria-regina	2n = 30 = 20V + 10I = 25V
P. liemianum	2n = 32 = 18V + 14I = 25V
P. chamberlainianum	2n = 34 = 16V + 16I = 25V
P. glaucophyllum	2n = 36 = 14V + 22I = 25V

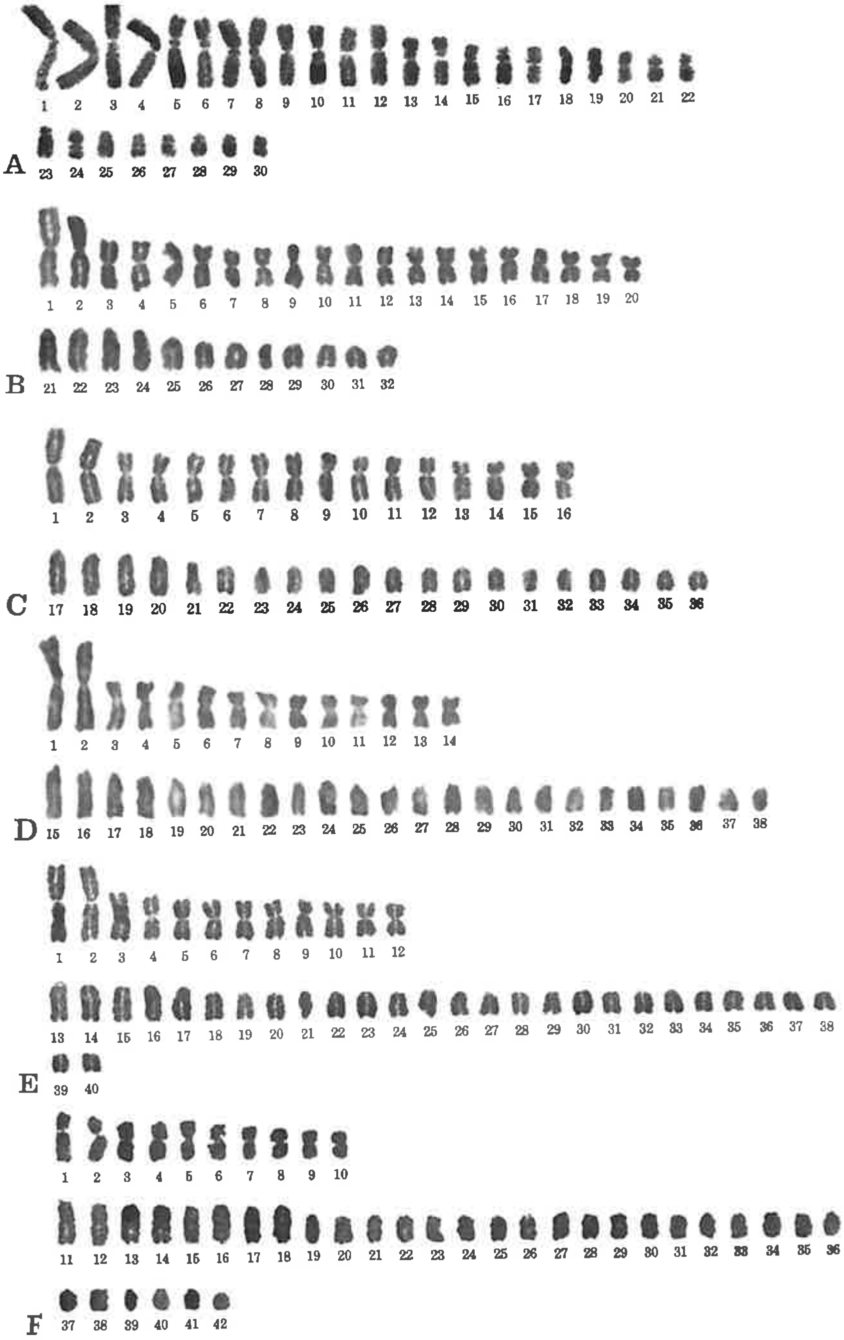

Fig. 18. Karyotype variations of the appreciated 2n=26V species.
A, *P. spicerianum.* B, *P. callosum.* C, *P. acmodontum.* D, *P. appletonianum.* E, *P. sukhakulii.* F, *P. celebesensis.* × 1000.

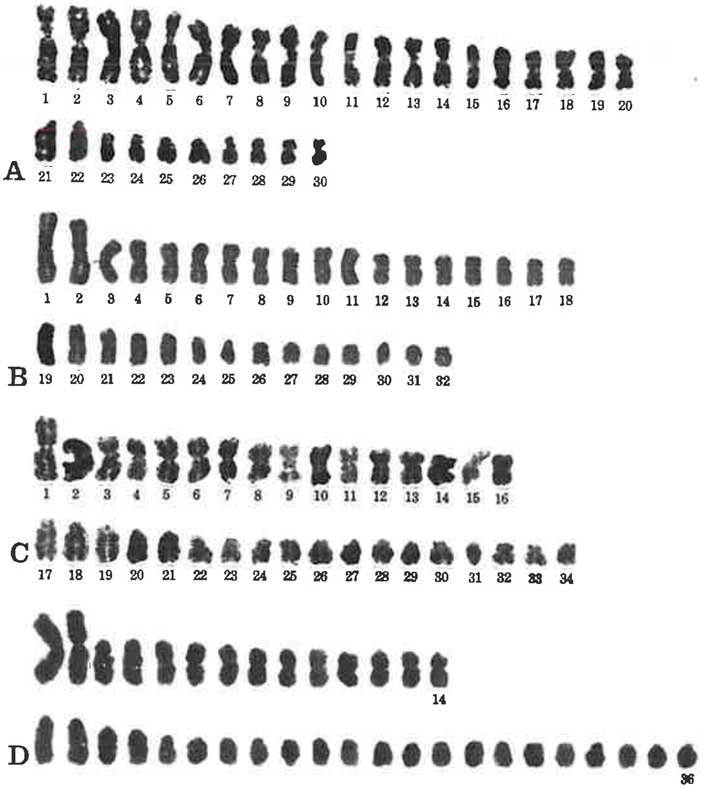

Fig. 19. Karyotype variations of the appreciated 2n=25V species.
A, *P. victoria-regina*. B, *P. liemianum*. C, *P. chamberlainianum*. D, *P. glaucophyllum*. x 1000.

The second type karyotype is considered to be derived from the loss of a pair of telocentric chromosomes occured by the centric fission.

Though the chromosome numbers in the genus varies greatly, the basic chromosome number is clearly n=13. And the species with chromosome 2n=28–42 are considered to be derived from 2n=26 by the increasing of chromosomes by centric fission or by subsequent loss of telocentric ones, and the 2n=25V type karyotype is different from the former type being derived from the loss of telocentric chromosomes (Karasawa 1969, Karasawa & Tanaka 1980).

With regard to the variation of the chromosome number, subgenus Parvisepalum, Brachypetalum and Polyantha are all 2n=26, while the chromosome number of the other subgenera (subgenus Paphiopedilum, Sigmatopetalum and Cochlopetalum) vary from 2n=26 to 2n=42. The wide variation in chromosome numbers in some subgenera seems to be that those subgenera are genetically differentiating or unstable at the present time, and the subgenera, of which chromosome numbers are uniform, seem to be not so active and much stable than the formers. With regard to the relation to geographical point of view, the karyotypes vary greatly at the marginal areas of their distributional ranges in various ranks of species assemblages.

Phylogeny indicated by characters

The morphological characters of vegetative organs (leaf, stem and stolon) in *Paphiopedilum* are mostly not correlated with each other and vary independently. Evolutionary tendencies of most characters of vegetative organs are understandable by the comparison of those characters with those of the other genera or families. But the phylogenetic trends of detailed characters of leaves, such as leaf thickness and density of stomata, are hardly recognizable because they are probably reflecting the habitat conditions rather than phylogenetic conditions.

The floral characters, on the other hand, are closely related with each other. Morphological features of lip have been regarded as of prime importance for the floral characters in the taxonomy of Orchidaceae. The various stages of lip evolution have been evaluated as very important by authors (Pfitzer 1903, etc.). However, there are close relations between the lip characters and those of the other floral characters in *Paphiopedilum,* and they seem to be also important in the *Paphiopedilum* taxonomy. Most of the variations of floral characters, as shape and nature of lip, and nature of pollinia, more or less correlate with the karyotype variations. Along with the increasing of chromosome numbers, the following general trends in floral

Table 5. Possible phyletic trends of characters.

Subgenus Characters	Parvisepalum	Brachypetalum	Polyantha	Paphiopedilum	Sigmatopetalum	Cochlopetalum	(Arrow indicate the direction of phyletic trends)
Stolon	+	–	–	–	–	–	Undifferentiated (+) ⟶ Differentiated (–)
Leaf	+	+	–	–	+	±	Green (–) ⟶ Mottled (+)
Number of flowers	+	±	–	+	+	–	Pluri-flowered (–) ⟶ Uni-flowered (+)
Habit of bloom	–	–	–	–	–	+	Simultaenously (–) ⟶ Separately (+)
Shape of perianth	–	–	+	+	+	+	Same shape (–) ⟶ Different shape (+)
Color of perianth	–	–	+	+	+	+	Same color (–) ⟶ Different color (+)
Lip shape	–	–	+	+	+	+	Calceolate (–) ⟶ Helmet shape (+)
Edge of lip	–	–	±	+	+	±	Incurved (–) ⟶ Recurved (+)
Ear of lip	–	–	±	+	+	+	Undifferentiate (–) ⟶ Differentiate (+)
Surface of perianth	–	+	+	+	+	+	Wrinkled (–) ⟶ Smooth (+)
Stigmata	–	+	+	+	+	+	Long-stalk (–) ⟶ Short-stalk (+)
Anther	–	+	+	+	+	+	Long-stalk (–) ⟶ Short-stalk (+)
Surface furrow of stigmata	–	+	+	+	+	+	Deep (–) ⟶ Shallow (+)
Pollinia	–	+	+	+	+	+	Granulous (–) ⟶ Viscous (+)
Seed shape	±	–	±	–	+	±	Oval (–) ⟶ Spindle shape (+)
Chromosome number	–	–	–	±	+	+	2n=26 (–) ⟶ 2n=42 (+)
Chromosome complement	–	–	–	–	–	+	2n=26V (–) ⟶ 2n=25V (+)

morphlology are found in this genus.

In this general trends, chromosome number and the floral characters vary in parallel. The tessellated leaves and the number of flowers on racemes do not correlate with the other floral structures, and it is considered as an useful criterion for separating the subgenera.

For the consideration of phyletic relationships of taxa, the possible phyletic trends are summarized on the basis of the preceeding discussions. The inferable primitive and derived conditions in each characters are listed in Table 5.

Taxonomy

Paphiopedilum Pfitzer, Morph. Stud. Orchideenbl.: 11 (1886).

Type species: *Paphiopedilum insigne* (Wall. ex Lindl.) Pfitz.

There have been proposed various concepts of *Paphiopedilum,* among which that of Rolfe (1896) is appreciated as a natural assemblage based on many morphological and chromosome characters as well as on the phylogenetic considerations. There also have been proposed various concepts as to the subdivision of *Paphiopedilum,* but none of them seem to recognize satisfactorily the intrageneric taxa, especially the subgenera. We recognize 6 subgenera, namely Parvisepalum, Brachypetalum, Polyantha, Paphiopedilum, Sigmatopetalum and Cochlopetalum.

Key to the subgenera of *Paphiopedilum*

1. Racemes pluri-florous ———— 2
1. Racemes uni– (rarely 2) florous ———— 3
2. Flowers opening out at the same time; leaves green, fleshy and leatherly; chromosome number 2n=26 ———— Polyantha
2. Flowers opening out simultaneously from lower portion to the tip of racemes, and always only one flower opening out on raceme; leaves greyish green, not fleshy, more or less grassy; chromosome numbers 2n=30–36 ———— Cochlopetalum
3. Leaves pale to deep green ———— Paphiopedilum
3. Leaves tessellated ———— 4
4. Lip not calceolate, more or less helmet-shaped; upper marginal portion almost straight or slightly recurved, auricles well differentiated; sepals much different from lateral petals in both shape and pattern; leaves tessellated with pale greyish to deep green portions and almost white portions; chromosome numbers 2n=28–42 ———— Sigmatopetalum
4. Lip more or less calceolate; upper marginal portion exauriculate, incurved; sepals more or less different from lateral petals in shape, but very similar in pattern; leaves tessellated with dark purplish green portions and pale greyish portions, abaxial surface of leaves always uniformly tinged with dark purple; chromosome numbers 2n=26 ———— 5
5. Pollinia granulous; lip distinctly calceolate; column elongated, stigma with deep grooves on surface; lateral petals much larger than upper sepal, spreading horizontally——Parvisepalum

5. Pollinia viscous; lip ovoid; stigmata rounded, with shallow grooves on surface; upper sepal slightly smaller than lateral petals; lateral petals spreading slightly downward ———— Brachypetalum

1. Subgenus **Parvisepalum** Karasawa et Saito, *subgen. nov.*

Subgen. Brachypetali similis, sed differt polliniis granulosis, stigmate longipedicellato, sepalis parvioribus quam petalis, labello calceolato gracile leviter plicato.

Type species: *Paphiopedilum delenatii* Guill.

The species of Parvisepalum are known only from North Vietnam and Yunnan of China, and it shows the smallest (limited) distributional area in this genus. Parvisepalum is closely similar to Brachypetalum in the following characters: 1) tessellated leaves, 2) uni-flowered inflorescence, and 3) 2n=26 chromosome numbers. But the Parvisepalum is clearly distinguished from Brachypetalum in the following features: 1) pollinia granulous, 2) stigmata much elongated, and long-stalked, 3) occurrence of stolon, 4) upper sepal much smaller than lateral petals, and 5) lip strongly calceolate, thin, grassy and faintly plicate. Except the occurrence of stolon, the subgeneric characters of Parvisepalum are apparently primitive features and not observed in the other subgenera, but most of them are common with those of genus *Cypripedium*. Though the subgenus Parvisepalum and Brachypetalum are very similar in appearance, they are well distinguished each other and considered to be evolved into slightly different directions. The geographical distributions of the species in this subgenus are restricted to the northern part of the Indo-Malayan area (Fig. 20). The species of Parvisepalum seem to be shifted combining with the evolution of leaf characters, decreasing of flower number and the differentia-

Fig. 20. Distributions of the species in subgenus Parvisepalum.
●, *P. delenatii.* ▲, *P. micranthum.* ■, *P. armeniacum.*

tion of stolon, retaining some primitive features (calceolate lip, long-stalked stigmata, and granulous pollinia). The species of Parvisepalum seem to be not so actively differentiating as of the other subgenera not only in the morphological features but also in the genetic conditions.

Key to species of subgen. Parvisepalum

1. Sepals and petals white, with deep purplish veins; lip strongly protruding — *P. micranthum*
1. Sepals and petals entirely plain, without veins; lip declivitous ———————— 2.
2. Sepals, petals and lip uniformly apricot yellow in color; basal portion of lip inner-surface dotted with purplish, minute spots ———————— *P. armeniacum*
2. Sepals, petals and lip uniformly pale pinkish-white in color; inner-surface of lip not dotted ———————— *P. delenatii*

* ***Paphiopedilum delenatii*** Guillaumin, Bull. Soc. Bot. France 21: 554. 1924.
* ***Paphiopedilum armeniacum*** Chen et Liu, Acta Botanica Yunnanica 4(2): 163–165 (1982).
* ***Paphiopedilum micranthum*** Tang et Wang, Acta Phytotaxonomica Sinica 1: 56–57 (1951).

2. Subgenus **Brachypetalum** Hall., Ann. Jard. Bot. Buitenzorg 14: 34 (1897).
Type species: *Paphiopedilum concolor* (Batem.) Pfitz.

This subgenus is very similar to Parvisepalum in some morphological characters as well as in chromosome numbers and karyotypes, though it is clearly distinguished from Parvisepalum in the following differences: 1) lip not calceolate, ovoid, thick, and plain on surface, 2) pollinia viscous 3) thick epidermis and high density of stomata on leaves, and 4) absence of stolon. Among these morphological characters of subgenus Brachypetalum, the viscous pollinia and the nature and shape of lip are considered to be derived features than those of Parvisepalum. Brachypetalum, on the other hand, have many primitive features which are common with those of Parvisepalum: 1) strongly incurved upper margin of lip, 2) undifferentiated lateral ears of lip, 3) oblong seeds, 4) close similarity of sepals and petals in color and shape, and the similar color pattern of lip with other perianth, and 5) 2n=26 chromosome numbers. Although the species of this subgenus are almost uniform in karyotype, each species is more or less showing morphological variations in some characters, especially in the floral characters. Wide intraspecific variations in this subgenus seem to suggest that the species of Brachypetalum are rather unstable in genetic conditions.

The Brachypetalum species are widely distributed in relativey southern part than Parvisepalum, and they are found in south of Burma, Thailand, Laos, Cambodia, Vietnam and Malay Penninsula (Fig. 21). In these areas, the plants are very frequently found.

Phylogenetically, Brachypetalum is apparently closely related to Parvisepalum in having many common characters which are mostly primitive characteristics, but Brachypetalum has evolved into different direction and is considered to be more advanced taxon because of the

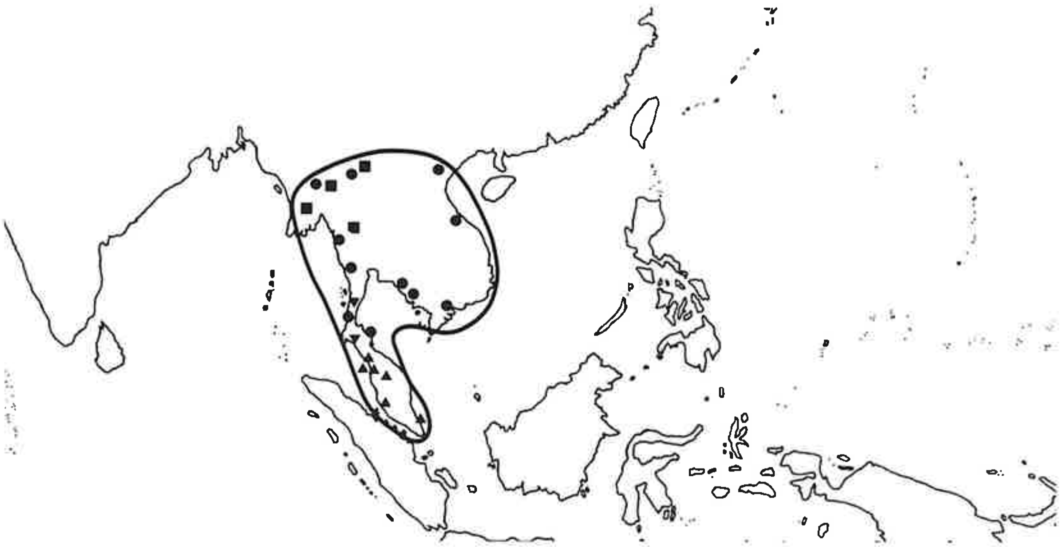

Fig. 21. Distributions of the species in subgenus Brachypetalum.
●, *P. concolor.* ■, *P. bellatulum.* ▲, *P. niveum.* ▼, *P. leucochilum*

viscous pollinia and ovoid lip. In addition, the presence of many transitional species indicates that Brachypetalum is inferable as an active species assemblage.

Key to species of subgen. Brachypetalum

1. Perianth pale yellow: upper sepal and petals finely and sparsely speckled with minute, deep purple spots: lip narrow ovoid, more or less pointed at tip ——— *P. concolor*
1. Perianth white or faintly tinged with pale purple: lip ovoid to broad-ovoid, hardly pointed at tip ——— 2
2. Petals and sepals almost plain in color, but faintly speckled only at the basal portions with minute, pale purple spots: peduncles long, more than 5 cm long ——— *P. niveum*
2. Petals and upper sepal distinctly dotted with large, deep purple speckles: peduncle short, usually 2–5 cm long ——— 3
3. Lip irregularly and sparsely speckled with large deep purplish spots: large speckles on petals and sepal irregularly scattered: peduncle very short, 2–3 cm long ——— *P. bellatulum*
3. Lip hardly speckled, almost plain, whitish: small speckles on petals and sepal arranged in lines: peduncle 3–5 cm long ——— *P. leucochilum*

* ***Paphiopedilum concolor*** (Batem.) Pfitz., Engl. et Prantl, Nat. Pflanzenfam. ii, 6: 84 (1888).
– *Cypripedium concolor* Batem., in Hook. Bot. Mag., 91, t. 5513 (1865).

* ***Paphiopedilum bellatulum*** (Reichb. f.) Stein, Orchideenbuch, 456 (1892).
– *Cypripedium bellatulum* Reichb. f., Gard. Chron. 1: 746–747 (1888).

* ***Paphiopedilum leucochilum*** (Rolfe) Fowl., Orch. Dig., 39 (3): 110–118 (1975).
– *Cypripedium godefroyae* var. *leucochilum* Rolfe, *auct, non* Godefroy-Lebeuf., Orch, Rev., II: 145 (1894).

* ***Paphiopedilum niveum*** (Rchb. f.) Stein., Orchideenbuch, 478 (1892).
– *Cypripedium niveum* Reichb. f., Gard. Chron. II: 1038 (1869).

Note : *Paphiopedilum godefroyae* has long been treated as an independent species, but the close observation of karyotype by Karasawa (1979) revealed that it is a natural hybrid between *P. concolor* and *P. bellatulum.*

3. Subgenus **Polyantha** (Pfitz.) Brieg., Orchideen 175 (1971)
Type species: *Paphiopedilum lowii* (Lindl.) Pfitz.
– Sect. *Polyantha* Pfitz., Engl. Bot. Jahrb. 19: 41 (1894) – Subgen. *Anotopedilum* Pfitz., Engl. Pflanzenreich IV. 50: 58 (1903).

In the taxonomy of *Paphiopedilum,* the differentiation of the lateral ears of lip has long been regarded as the most important character in classifying the genus into two subgenera (Pfitzer 1901, Asher 1980–81, etc.). And they classified the species of broad sense of Polyantha (Brieger 1971) into two subgenera, such as Anotopedilum and Otopedilum (Pfitzer 1903). Similar evolutional trend of lip simplification is observed in *Phragmipedium* : for example, lip of *P. schlimii* is distinctly calceolate and having no ears on it, while lip of *P. longifolium* is not calceolate and having distinct ears on it. As discussed before (p. 15), the presence of lateral ears is considered to be an extreme form of the simplification series of lip and should

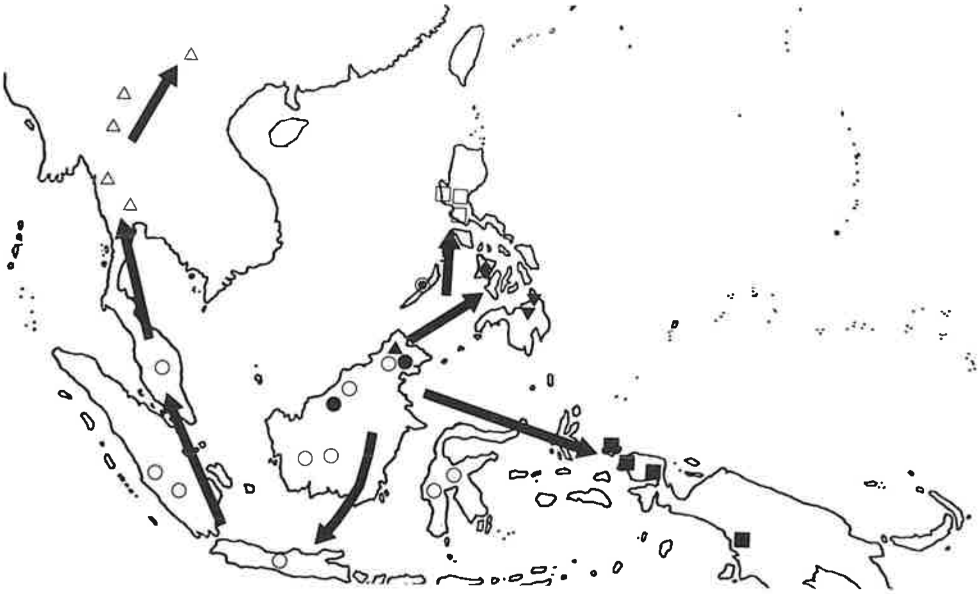

Fig. 22. Possible speciation course of the species in subgenus Polyantha.
●, *P. stonei.* ▲, *P. rothschildianum.* ♦, *P. philippinense.* ▼, *P. randsii.* ■, *P. praestans.* ⊙, *P. elliottianum.* ○, *P. lowii,* □, *P. haynaldianum.* △, *P. parishii.*

not be employed as the criterion in recognizing the subgenera. Subgenus Polyantha is well recognized as a natural taxon and distinguished from the rest subgenera by the following combination of the characters: 1) pluri-flowered inflorescence, 2) simultaneous spreading of the flowers, 3) green, thick and leathery leaves, 4) oblong seeds, and 5) 2n=26=26V chromosome numbers. Addition to the above mentioned characteristics, the simplification series of lip and the differentiation series of both sepals in shape, size and color patterns within this subgenus seem to suggest the continuation of those species and the independency of the subgenus as a natural taxon.

Phylogenetically, subgenus Polyantha is apparently closely related to subgen. Paphiopedilum because of the common features of leaves, and it is inferable to be relatively primitive than subgen. Paphiopedilum in the pluri-flowered inflorescens and the presence of simplification series of lip. Those external morphological characters and the karyotypes of Polyantha are definitely exhibiting that Polyantha is closely related to the ancestral stock of subgen. Paphiopedilum but differs from it in the well specialized lateral petals in shape, size and color patterns. Pluri-flowerd inflorescence and the well specialized lateral petals in Polyantha, on the other hands, are considered to be suggesting the close relationships of the subgenus Polyantha to subgen. Cochlopetalum (see discussion of Cochlopetalum).

The shape of auricle and the direction of margin of their pouch vary in shape, and also the karyotypes of each species vary greatly at the marginal areas of their distributional ranges (Fig. 22, Table 6).

There are three sections in subgen. Polyantha: they are sect. Mastigopetalum, Polyantha and Mystropetalum.

Table 6. Species, characters and distribution of subgenus Polyantha.

Characters / Species	Form of lip*		Chromosome number of arm ratio over 1.5 (over 1.7)	Distribution
	Edge	Ear		
P. stonei	–	–	0	Borneo
P. rothschildianum	–	–	0	Borneo
P. praestans	–	–	3	West Irian
P. philippinense	–	–	12	Philippine
P. randsii	–	+	5	Philippine
P. elliottianum	+	–	8	Philippine
P. haynaldianum	+	+	14	Philippine
P. lowii	+	+	14	Borneo, Sumatra Malay Peninsula
P. parishii	+	+	18 (6)	Thailand
P. parishii var. dianthum	+	+	10 (10)	Yunnan

* Edge : Incurved (–) → Recurved (+), Ear : Undifferentiated (–) → Differentiated (+).

Key to sections of subgen. Polyantha

1. Upper and lower sepals almost same in shape, size and color patterns: lip upper margin strongly incurved or ear not differentiated ——— Mastigopetalum
1. Upper and lower sepals clearly differentiated in shape, size and color patterns; lip upper margin not incurved straight or slightly outward; ear well developed ——— 2
2. Lateral petals gradually widened toward apex, narrow spoon-shaped, spreading slightly downward, hardly contorted ——— Polyantha
2. Lateral petals gradually narrowed toward apex, linear, strongly twisted and drooping ——— Mystropetalum

Sect. **Mastigopetalum** Hall. Ann. Jard. Buitenzorg. 14: 44 (1896).

Type species: *Paphiopedilum stonei* (Hook. f.) Pfitz.

– Sect. *Gonatopetalum* Pfitz., Engl. Pflanzenreich IV. 50: 62 (1903).

Some of the previous authors (Pfitzer 1903, Brieger 1971, etc.) regarded the differences of staminode as the important criterion in classifying the species of subgenus Polyantha (sensu stricto), and they classified subgen. Polyantha (sensu stricto) into five sections, such as sect. Gonatopedilum, Prenipedilum, Coryopedilum, Mystropedilum and Pardalopedilum based mainly on the differences of staminode morphology as well as of lip. But as discussed before, the differentiations of staminode do not necessarily reflect the phylogenetic relationships between the taxa in subgen. Polyantha. Section Mastigopetalum is well recognized by the uniformity of both sepals in sharing the common features, and moreover the absence of lateral ears of lip (except in *P. randsii*) suggest that the section is monophyletic species assemblage.

Sect. Mastigopetalum is considered to be the most primitive taxon within subgen. Polyantha because of the undifferentiation of both sepals and the undifferentiation of lateral ears of lip.

Key to species of sect. Mastigopetalum

1. Margin of lip more or less recurved; staminode inclined upward ——— *P. elliottianum*
1. Margin of lip distinctly incurved; staminode not inclined upward ——— 2
2. Lip exauriculate at mouth; lateral petals short, not twisted, beautifully striped; margin of lateral petals with no warts ——— *P. randsii*
2. Lip not exauriculate at mouth; lateral petals linear, more or less twisted or contorted, usually with dots and stripes: margins of lateral petals with black ciliate warts ——— 3
3. Staminode narrow, geniculately protruded, terete beneath the knee, under side of apical portion long hairly ——— *P. rothschildianum*
3. Staminode broad, not geniculately protruded ——— 4
4. Lateral petals very long, 50–60 cm long ——— *P. sanderianum*
4. Lateral petals shorter, less than 20 cm long ——— 5

5. Staminode oblong, without protuberance at middle; petals obliquely dependent, narrow linear-falcate ——— *P. stonei*
5. Staminode rounded quadrangle or obovate: petals straightly bending, more or less strongly twisted ——— 6
6. Staminode rounded quadrangle, with minute horn-shaped protuberances at both upper ends ——— *P. praestans*
6. Staminode obovoid, without protuberance ——— *P. philippinense*

* ***Paphiopedilum elliottianum*** (O'Brien) Stein, Orchideenbuch 466 (1892).
 – *Cypripedium elliottianum* O'Brien, Gard. Chron. 2: 501, 532 (1888).

* ***Paphiopedilum philippinense*** (Reichb. f.) Stein, Orchideenbuch 480 (1892).
 – *Cypripedium philippinense* Reichb. f., Bonplandia 335 (1862). – *Paphiopedilum roebbelinii* (Reichb. f.) Pfitz., Engl. Bot. Jahrb. 19: 44 (1894). – *Cypripedium roebbelinii* Reichb. f., Gard. Chron. 2: 684 (1883). *syn. nov.* – *Paphiopedilum leavigatum* (Batem.) Pfitz., Engl. & Prantl., Naturl. Pfanzenfam. ii 6: 84 (1888). – *Cypripedium laevigatum* Batem., Bot. Mag. t. 5508 (1862).

* ***Paphiopedilum praestans*** (Reichb. f.) Pfitz., Engl. Bot. Jahrb., 19: 41 (1894).
 – *Cypripedium praestans* Reichb. f., Gard. Chron. 2: 766 (1886).

* ***Paphiopedilum randsii*** Fowl., Orch. Dig. 33 (10): 321–322 (1969).

* ***Paphiopedilum rothschildianum*** (Reichb. f.) Stein, Orchideenbuch 482 (1892).
 – *Cypripedium rothschildianum* Reichb. f., Gard. Chron. 1: 457, 544 (1888).

* ***Paphiopedilum sanderianum*** (Reichb. f.) Stein, Orchideenbuch 482 (1892).
 – *Cypripedium sanderianum* Reichb. f., Gard. Chron. 1: 554 (1886).

* ***Paphiopedilum stonei*** (Hook. f.) Stein, Orchideenbuch 487 (1892).
 – *Cypripedium stonei* Hook. f., Bot. Mag. t. 5349 (1862).

Note: As closely discussed by Asher (1981), *P. glanduliferum* is distinguished from *P. praestans* in many morphological differences. Karasawa (1979), on the other hand, examined the detailed features of chromosomes of the living plants of *P. glanduliferum* (identified by Rands). As regard to the external morphologies and the karyotype, *P. glanduliferum* of Rands was well distinguished from *P. praestans.* But the authentic plants of *P. glanduliferum* is known only in the original one and has not been colloected in recent time in spite of many field investigations of north-west areas of New Guinea. We are afraid to treat *P. glanduliferum* as an independent taxon in this study.

Sect. **Polyantha**

Type species: *Paphiopedilum lowii* (Lindl.) Stein

Section Polyantha is well distinguished from related sections by the presence of lateral ears of lip and narrow spoon-shaped lateral petals, of which basal to middle portion is roughly blotched with deep purple dots. Not only those characteristics of sect. Polyantha, the differentiation of upper and lower sepals in shape, size and color patterns as well as the presence of many chromosomes whose arm ratio is more than 1.5, are all considered to be relatively derived features. And sect. Polyantha is inferable as a derived taxon from sect. Mastigopetalum through the floating of distributional range from islands to continent as well as the differentiation of morphological characters of this subgenus.

Key to species of sect. Polyantha

1. Upper sepal without brownish blotches, almost plain throughout ——————— *P. lowii*
1. Upper sepal with large brownish blotches at basal portion ——————— *P. haynaldianum*

* ***Paphiopedilum lowii*** (Lindl.) Stein, Orchideenbuch, 476 (1892).
– *Cypripedium lowii* Lindl., Gard. Chron., 765 (1847).
* ***Paphiopedilum haynaldianum*** (Reichb. f.) Stein, Orchideenbuch, 470 (1892).
– *Cypripedium haynaldianum* Reichb. f., Xenia Orch. 2: 222 (1874).

Sect. **Mystropetalum** Pfiz. Engl. Pflanzenreich, IV. 50: 65 (1903).

Type species: *Paphiopedilum parishii* (Reichb. f.) Stein

This section is very similar to sect. Polyantha in the presence of lateral ears of lip, the differentiation of upper sepal from lower one, and the occurrence of many chromosomes whose arm ratio is more than 1.5. Geographically, sect. Mystropetalum is well different from the rest sections in distributional range; the species is found in continental areas, such as from northern part of Indo-Malayan continent to south of China through north of Burma. Sect. Mystropetalum is well distinguished from sect. Polyantha in the linear, strongly twisted lateral petals. Most characteristics of sect. Mystropetalum are, as discussed before, considered to be derived features, and Mystropetalum seems to be a derived taxon from sect. Mastigopetalum.

* ***Paphiopedilum parishii*** (Reichb. f.) Stein, Orchideenbuch, 479 (1892).
– *Cypripedium parishii* Reichb. f., Flora lii: 322 (1869).
* var. ***dianthum*** (Tang & Wang) Karasawa et Saito, *stat. nov.*
Paphiopedilum dianthum Tang & Wang, Bull. Fan. Mem. Inst. Biol. Peiping, Bot. Ser. X: 23 (1940)

Paphiopedilum dianthum Tang & Wang was described from south of China (Yunnan) and was characterized by less brownish color, usually more shiny floral parts, more conical shape of pouch and glabrous ovary. The detailed observation of chromosomes revealed that *P. dianthum* is apparently different from *P. parishii* in the number of chromosomes of which arm ratio is more than 1.5. Though the karyotype of *P. dianthum* and the external morphology of *P. dianthum* are slightly different from those of *P. parishii*, we are not sure in recognizing *P. dianthum* as an independent taxon.

4. Subgenus **Paphiopedilum**

Type species: *Paphiopedium insigne* (Wall. ex Lindl.) Pfitz.

The phylogenetic relationships of subgen. Paphiopedilum to other subgenera seem to be easily recognizable by the following characteristics: 1) uni-flowered racemes, 2) green leaves, and 3) well developed lateral ears of lip upper margin. The features of this subgenus apparently suggest the close relationship to subgen. Polyantha, and the uni-flowered racemes and the detailed morphology of lip indicate that the subgen. Paphiopedilum is a derivative from Polyantha. With regard to the karyotype, subgen. Paphiopedilum is essentially a same type with that of subgen. Polyantha in 2n=26V, though there are many variations in both of number and karyotype. In addition, the species of this subgenus have not been discovered in Borneo, Java, Sumatra, Philippines and their adjacent islands, but they are abundant in Indo-Malayan Continent, India and adjacent regions (Fig. 23). In these areas, the species having most primitive karyotype (*P. exul*) is distributed in southern parts of Thailand, where is the marginal part of distribution area of subgen. Polyantha. In this subgen. the speciation have probably been taken out connecting with the differentiations of karyotype: karyotype has evolved by the changing of arm ratio of chromosomes and the increasing of chromosome numbers by centric fission.

Though the phyletic relationships of subgen. Paphiopedilum to the other subgenera is easily understandable and the subgenus is well recognized as a natural assemblage, there are many phyletic lines within this subgenus (Fig. 23). They are sect. Stictopetalum, Paphiopedilum, Ceratopedilum, and Thiopetalum. These sections are distinguished each other by the differences in detailed morphology of flowers.

Fig. 23. Possible speciation courses in subgenus Paphiopedilum.
●, *P. exul.* ■, *P. villosum.* ♦, *P. charlesworthii.* ▲, *P. insigne.* ▼, *P. druryi.* ⊙, *P. hirsutissimum.* ○, *P. spicerianum*

Key to sections of subgen. Paphiopedilum

1. Lateral petals gradually widened toward apex —— Paphiopedilum
1. Apical portion of lateral petals not wider than the middle portion —— 2
2. Lateral petals linear-lanceolate, somewhat drooping, strongly distorted backward at apex; upper sepal distinctly striped, stripes more or less connecting in marginal portion —— Ceratopetalum
2. Lateral petals lanceolate to spathulate, apical portion not distorted backward: upper sepal not striped by many vertical lines —— 3
3. Lateral petals spreading directly, but more or less twisted in the apical portion: lateral petals and upper sepal without distinct thick line at the middle: chromosome number 2n=26 —— Stictopetalum
3. Lateral petals strongly incurved, not twisted in the apical portion: lateral petals and upper sepal with distinct, thick line at the middle: chromosome number 2n=30 —— Thiopetalum

Sect. **Stictopetalum** Hall., Ann. Jard. Buitenzorg 14: 40 (1894).

Type species: *Paphiopedium hirsutissimum* (Lindl. ex Hook.) Stein

Sect. Stictopetalum is well characterized by the long, slightly constricted lip, broad lanceolate, vertically spreading and more or less sinuating lateral petals, distinct undulations at basal to middle portion of upper margin of the lateral petals, and dense hairiness on whole surface of flower.

* ***Paphiopedilum hirsutissimum*** (Lindl.) Pfitz., Engl. Bot. Jahrb. 19: 41. (1894).
–*Cypripedium hirsutissimum* Lindl., Curtis Bot. Mag. 83, t. 4990 (1857). –*Paphiopedilum chiwuanum* Tang et Wang, Act. Phytotax. Sinica 1(1): 56 (1951)

* ________ var. ***esquirolei*** (Schltr.) Karasawa et Saito, *stat. nov.*
– *Paphiopedilum esquirolei* Schltr., Fedde Rep. Beih. 4: 39, 86 (1919).

Paphiopedilum esquirolei Schltr. is described from south of China and recently found also from northern east area of Thailand, and it is well characterized by the following characters: 1) leaves leatherly, linear, 15–20 mm in width, and bright green, 2) basal portion of abaxial surface not tinged with deep purple, 3) dorsal sepal deep blackish purple with green margin, 4) scape and floral part covered with only a few hairs, and 5) short ovary.

Addition to the external morphological differences, the karyotype of this taxon is entirely different in comprising 26 metacentric chromosomes, and we think that *P. esquirolei* is well recognizable as an independent taxon of variety rank.

Sect. **Paphiopedilum**

Type species: *Paphiopedilum insigne* (Wall. ex Lindl.) Pfitz.

Sect. Paphiopedilum is the largest species assemblage within this subgenus, and well characterized by the following characteristics: 1) narrow spathulate lateral petals, 2) shorter lip, 3) obcordate staminode, with horn-shaped protuberance, and 4) $2n=26$ chromosome number. Though there is a small variation, the color patterns of upper sepal and lateral petals in most species seem to be essentially a blotch type, and the color pattern of *P. charlesworthii* is exceptionally plain throughout. Fewer number of chromosomes and the distribution area of the species of this section seem to suggest the comparatively closer relationships to sect. Stictopetalum than to sect. Thiopetalum.

Key to species of sect. Paphiopedilum

1. Upper sepal much widened, almost rounded, not blotched, uniformly tinged with reddish purple, gradually deeper toward base ——— *P. charlesworthii*
1. Upper sepal broad obovate, white in marginal portion, green in middle portion, roughly blotched or tinged with dark brown at middle to basal portion ——— 2
2. Lateral petals much widened toward apex from narrower base, evidently unequal-sided ——— *P. villosum*
2. Lateral petals otherwise, not so strongly widened, more or less equal-sided ——— 3
3. Lower sepal much shorter and narrower than upper sepal ——— *P. insigne*
3. Lower sepal subequalling with upper sepal in shape and size ——— *P. exul*

* ***Paphiopedilum charlesworthii*** (Rolfe) Pfitz., Engl. Bot. Jahrb. 19: 40 (1894).
– *Cypripedium charlesworthii* Rolfe, Orch. Review 1: 303 (1893).

* ***Paphiopedilum exul*** (O'Brien) Pfitz., Engl. Pflanzenreich, IV 50: 74 (1903).
– *Cypripedium exul* O'Brien, Gard. Chron. 1: 522, f. 77 (1892).

* ***Paphiopedilum insigne*** (Wall. ex Lindl.) Pfitz., Engl. & Prantl., Pflanzenfam. 2(6): 84(1889).
– *Cypripedium insigne* Wall. ex Lindl., Coll. Bot. t. 32 (1821).

* ***Paphiopedilum villosum*** (Lindl.) Stein, Orchideenbuch 490 (1892).
– *Cypripedium villosum* Lindl., Gard. Chron. 135. (1854). – var. *boxallii* (Reichb. f.) Veitch., Man. Orch. Pl. 4: 4 (1889). – *Cypripedium boxallii* Reichb. f., Gard. Chron. 1: 367, c. fig. II. 796 (1877).

Sect. **Thiopetalum** Hall., Ann. Jard. Buitenzorg 14: 39 (1896).

Type species: *Paphiopedilum druryi* (Beddome) Stein

Sect. Thiopetalum is very similar to sect. Paphiopedilum in many morphological characters: they are almost same with each other in shape of lip and lateral petals. Noteworthy differences between the sections are the presence of a single, distinct and broad center line on upper sepal and lateral petals and $2n=30$ chromosome numbers. The karyotype of the species of sect. Thiopetalum is $2n=30=22V+81$ and considered to be derived from $2n=26$ by centric fission of the chromosomes. Moreover, the species of sect. Thiopetalum are distributed in Burma to South India through Assam and Eastern India. These features of both external morphology and karyotypes seem to suggest that sect. Thiopetalum is a derived taxon from

Paphiopedilum by the differentiation in floral structure and chromosome morphology associating with the adaptation to new habitats of new areas.

Key to species of sect. Thiopetalum

1. Leaves up to 20 cm long: upper half of dorsal sepal white, green in lower half, with a single, thin vertical stripe at middle: upper margin of petals strongly undulate: pouch tinged with dark brown: staminode rhomboid, strongly incurved in upper part, slightly protruded at middle, tinged with purple ——— *P. spicerianum*
1. Leaves more than 20 cm long: dorsal sepal green throughout, with a single, thick brown vertical stripe: upper margin of lateral petals hardly undulate: pouch yellow: staminode cordiform, tinged with yellow ——— *P. druryi*

* ***Paphiopedilum druryi*** (Beddome) Stein, Orchideenbuch 466 (1892).
  – *Cypripedium druryi* Beddome, Icon. Plant. Ind. Orient. 23 t, 112 (1868).
* ***Paphiopedilum spicerianum*** (Reichb. f.) Pfitz., Engl. Bot. Jahrb. 19: 41 (1894).
  – *Cypripedium spicerianum* Reichb. f., Gard. Chron. 2: 40 363 (1880).

Sect. **Ceratopetalum** Hall., Ann. Jard. Buitenzorg 14: 39 (1896).

Type species: *Paphiopedilum fairrieanum* (Lindl.) Pfitz.

Sect. Ceratopetalum is a monotypic section including only *P. fairrieanum* and well distinguished from the other sections by almost vertically pendulous lateral petals, of which apical portions are strongly recurved backward, and by the thick, blackish purple longitudinal stripes. Brieger (1971) treated *P. fairrieanum* as of subgen. Barbata (=subgen. Sigmatopetalum) probably based on the ciliate petal margin, but the green leaves, high density of stomata, and the karyotype apparently suggest the section belonging to subgen. Paphiopedilum. The distributional range of *P. fairrieanum* is southern parts of Himalayas (Assam, Bhutan and Sikkim) and sharing common areas with the rest species of this subgenus.

* ***Paphiopedilum fairrieanum*** (Lindl.) Pfitz., Engl. Bot. Jahrb. 19: 41 (1894).
  – *Cypripedium fairrieanum* Lindl., Gard. Chron. 740 (1857).

5. Subgenus **Sigmatopetalum** Hall., Ann. Jard. Buitenzorg 36 (1896).

Type species: *Paphiopedilum venustum* (Wall.) Pfitz.
– Subgen. *Barbata* Kränzlin, Orch. Gen. Sp. 53 (1901).

Taxonomic concept of this taxon has been precisely circumscribed by Brieger (1971) and is considered to be a natural assemblage as discussed below, but he carelessly adapted the name 'Barbata' of Kränzlin (1901). Kränzlin (1901) treated sect. Barbata as a member of Cypripedium, and it included some species of subgen. Polyantha (sensu str.). On the other hand, the subgeneric concept of Brieger (1971) is including three sections of Hallier (1896), such as Sigmatopetalum, Clinopetalum and Drepanopetalum. Therefore, we have to adopt name Sigmatopetalum as a subgeneric name for this taxon based on the nomenclatural codes.

The subgenus Sigmatopetalum is the largest subgenus in *Paphiopedilum* including 24 species and similar to subgenera Parvisepalum and Brachypetalum in the tessellated leaves and in uni-flowered racèmes and well developed lateral ears of upper margin of lip. However Sigmatopetalum is entirely different from the other subgenera in the following combination of the characters: 1) uni-flowered racemes, 2) tessellated leaves, 3) well developed lateral ears of lip, acters: 1) uni-flowered racemes, 2) tessellated leaves, 3) well developed lateral ears of lip, 4) low density of stomata (12–26/mm^2), and 5) much smaller and more or less longitudinally striped lower synsepal. The karyotype of Sigmatopetalum is also noteworthy in recognition of the phylogenetic relationships with other subgenera. The karyotype of this subgenus is essentially 2n=26V (Karasawa 1979), but the chromosome numbers vary from 2n=28 to 2n=42. Those heteroploidy within this subgenus is considered to be caused in the increasing of chromosome numbers through centric fissions (Karasawa 1979).

The phylogenetic interrelationships of Sigmatopetalum to the other subgenera is very ambiguous, and there seems to be neither useful clue nor evidence. The most of the important features of Sigmatopetalum are sharing with subgen. Paphiopedilum except in tessellated leaves and low density of stomata. The all of the above mentioned characteristics of Sigmatopetalum are considered to be derived ones, and the subgenus is inferable as the most differentiated species assemblage within the genus *Paphiopedilum.*

In Sigmatopetalum, there are some differentiation series of characters: such as 1) petal widening series in sect. Blephalopetalum, 2) upper sepal widening series in subsect. Barbata,

Fig. 24. Distributions of the species in subgenus Sigmatopetalum.

and 3) increasing series of marginal cilia in subsect. Loripetalum.

Those evolutionary series of characters seem to closely related with the divergence (differtiation) of karyotype. The floral characters of primitive species in each series are more or less similar to those of subgen. Paphiopedilum species in appearance (e.g. *P. mastersianum*) than to those of the species of rest subgenera. And vast variation series of floral characters seem to suggest that Sigmatopetalum is derived from subgen. Paphiopedilum through multi-phyletic lines.

Not only the species of this subgenus show the wide range of intraspecific variations, but the species are also usually more or less similar to each other in morphological and karyomorphological characters. In addition, each species of subgenus are not distributed in the wide ranges but limited to relatively restricted areas. (Fig. 25, 27, 28). This make the taxonomy of Sigmatopetalum very difficult, and the taxonomic concepts of various ranks of taxa have not yet been precisely understood. Although it is very difficult to clarify all the phyletic relationships within Sigmatopetalum, we recognize following six sections based on the morphological characters as well as the possible phyletic (and speciation) lines. Six sections in Sigmatopetalum are Spathopetalum, Blephalopetalum, Punctatum, Barbata, Planipetalum and Sigmatopetalum.

Key to sections of subgen. Sigmatopetalum

1. Under surface of leaves tinged with dark purple throughout; leaf upper surface tessellated with pale greyish green parts and deep purplish green parts —— Sigmatopetalum
1. Under surface of leaves pale green throughout, or slightly tinged with deep purple at base: leaf upper surface tessellated with pale greyish or almost white parts and green parts —— 2.
2. Lateral petals knife-shaped, more or less widened in apical portion, margin slightly undulate at middle; upper sepal greenish, margin of upper half strongly incurved, longitudinal stripes indistinct, deep green in color —— Spathopetalum
2. Lateral petal shape otherwise, margin not undulate throughout: upper sepal white or purplish, margin of upper half not incurved, almost straight or slightly recurved, longitudinal stripes distinct, deep green or deep purple —— 3
3. Lateral petals without large, more or less swollen, distinct spots, almost same width from base to tip, upper halves usually deeper in color than lower halves —— Blephalopetalum
3. Lateral petals with large, more or less swollen deep purple spots, almost same color throughout —— 4
4. Lateral petals hardly ciliate, almost entire throughout, narrow spathulate, gradually widened toward apex; flower pale brown in color —— Punctatum
4. Lateral petals regularly or irregularly ciliate, narrow oblong or linear oblong; flower others in color —— 5
5. Lateral petals narrow oblong, almost same width from base to apex, not twisted, horizontally spreading; staminode more or less lunate —— Planipetalum
5. Lateral petals linear oblong, gradually narrowed toward apex, slightly declivitous; staminode semicircular or oblong —— Barbata

Sect. **Spathopetalum** Pfitz., Pflanzenreich IV, 50: 78 (1903).

Type species: *Paphiopedilum appletonianum* (Gow.) Rolfe

Section Spathopetalum is different from the other sections in the following combination of the characters: 1) longitudinal stripes on upper sepal indistinct, 2) margin of upper sepal strongly incurved in upper half, 3) margin of lateral petals almost entire, rarely ciliate only at base, 4) lateral petals knife-shape, much widened just behind the apex, and 5) staminode rounded or oblong rhomboid.

There are two subsections in sect. Spathopetalum, such as subsect. Macronodium and subsect. Spathopetalum. Subsect. Macronodium is a monotypic taxon and well characterized by the rounded, extraordinarily large staminode, the presence of long cilia on basal marginal portion of lateral petals, and the minute blotches on basal to median portion of lateral petals, while subsect. Spathopetalum is distinguished by the small, oblong rhomboid staminode, the absence of long cilia on lateral petal margin, and the presence of large, distinct dots on marginal portion of lateral petals. Karasawa (1979) clarified that there is a noteworthy phyletic line of karyotype in subsect. Spathopetalum: that is the increasing series of chromosome numbers by centric fission. Chromosome number of *P. appletonianum* is the smallest 2n=38, that of *P. bullenianum* (=*P. linii*) 2n=40, and that of *P. celebesensis* is 2n=42. These morphological and karyological features of this subsection seem to suggest that this taxon is a monophyletic, natural species assemblage.

Karyotype of *P. hookerae* of subsect. Mocronodium is quite different from those of subsect. Spathopetalum in 2n=28 chromosome number, and the karyotype of *P. hookerae* is inferable to be a relatively primitive than those of subsect. Spathopetalum.

The possible speciation courses of sect. Spathopetalum species are showen in Fig. 25.

Fig. 25. Possible speciation courses in sect. Spathopetalum.
●, *P. bullenianum*. ■, *P. hookerae*. ♦, *P. celebesensis*. ▲, *P. appletonianum*.

Key to subsections of sect. Spathopetalum

1. Staminode well developed, large, rounded (12–14 mm in diam.) : lateral petals with fine spots from base to middle: usually with long, black hairs on basal margin ———— Subsect. Macronodium
1. Staminode oblong rhomboid, relatively small (5–8 mm in diam.) : lateral petals with brownish spots on basal margin: basal margin with short, minute cilia ———— Subsect. Spathopetalum

Subsect. **Macronodium** Karasawa et Saito, *subsect. nov.*

Subsect. Spathopetali similis, sed differt staminodio grandis, petalis margine ciliatis et maculatis e basi ad midium.

Type species: *Paphiopedilum hookerae* (Reichb. f.) Pfitz.

* ***Paphiopedilum hookerae*** (Reichb. f.) Pfitz., Engl. Bot. Jahrb. 19: 41 (1894).
– *Cypripedium hookerae* Reichb. f., Xen. Orchid. II. 125, t 141 (1874). – *Paphiopedilum kookerae* var. *volonteanum* (Sand.) Kercheve, Orch. 456 (1894). – *Cypripedium volonteanum* Sand., Gard. Chron. 2: 7 (1890). – *Paphiopedilum volonteanum* (Sand.) Pfitz., Engl. Pflanzenreich, 4, 50: 80 (1903).

Subsect. **Spathopetalum**

Type species: *Paphiopedilum appletonianum* (Gow.) Rolfe

Key to species of subsect. Spathopetalum

1. Pouch pot-shaped, gradually narrowed toward mouth: lateral petals knife-shape, much widened just behind the apex: chromosome number 2n=42 ———— *P. celebesensis*
1. Pouch long helmet-shaped, not narrowed at mouth, slightly constricted just below the mouth: lateral petals narrow oblong, gradually narrowed toward apex ———— 2
2. Staminode oblong, somewhat ladder-shape; petal marginal cilia white: chromosome number 2n=38 ———— *P. appletonianum*
2. Staminode oblong rhomboid: petal marginal cilia black: chromosome number 2n=40 ———— *P. bullenianum*

* ***Paphiopedilum appletonianum*** (Gow.) Rolfe, Orchid Review 4: 364 (1896)
– *Cypripedium appletonianum* Gow. Gard. 1: 95 (1893), – *Cypripedium wolterianum* Krzl., Xen. Orch. 3: 142, t. 282 (1896). – *Paphiopedilum wolterianum* (Krzl.) Pfitz., Engl. Pflanzenreich, 4. 50: 179 (1903) – *Cypripedium bullenianum* var. *appletonianum* Rolfe, Orch. Rev. 1: 135 (1893).

* ***Paphiopedilum bullenianum*** (Reichb. f.) Pfitz., Engl. Bot. Jahrb. 19: 40 (1894).
– *Cypripedium bullenianum* Reichb. f., Bot. Zeit., 99 (1865). – *Cypripedium hookerae*

Pfitz. var. *bullenianum* (Reichb. f.) Veitch, Man. Orch. Pl. 4: 32 (1889). – *Paphiopedilum hookerae* (Reichb. f.) Pfitz. var. *bullenianum* (Reichb. f.) Kerch., Orch. 454 (1894).

We regrettably could not examine the type specimens of *P. amabile, P. linii* and *P. johorensis.* We made a karyological study on the chromosomes of the plants which are just fit with the type descriptions, and could not find any difference in the chromosome number and karyotype. Judging from the descriptions and figures as well as the living plants, there seems to be no diagnostic differences between *P. bullenianum* and the rest species.

* ***Paphiopedilum celebesensis*** Fowl. et Birk, Orch. Dig. 44: 23–30 (1980).

Sect. **Blephalopetalum** Pfitz., Engl. Pflanzenreich 4(50): 82 (1903).

Type species: *Paphiopedilum mastersianum* (Reichb. f.) Stein

Sect. Blephalopetalum is rather similar to sect. Spathopetalum and sect. Punctatum, but it is different in the linear oblong leaves, the absence of minute dots on lateral petals (except in *P. mastersianum*), upper halves of lateral petals deeper in color than lower halves, and the semilunate to/or semi-orbiculate staminode. As observated in sect. Spathopetalum, there is also a distinct phyletic line of karyotype in sect. Blephalopetalum: that is the increasing series of

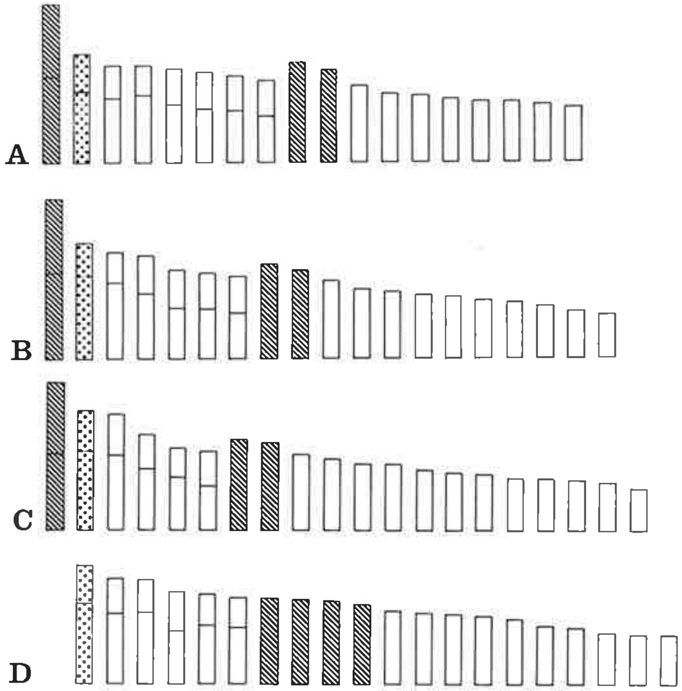

Fig. 26. Idiograms of haploid chromosome set of 4 species in sect. Blephalopetalum. A, *P. mastersianum* 2n=36. B, *P. violascens* 2n=38. C, *P. wentworthianum* 2n=40. D, *P. bougainvilleanum* 2n=40.

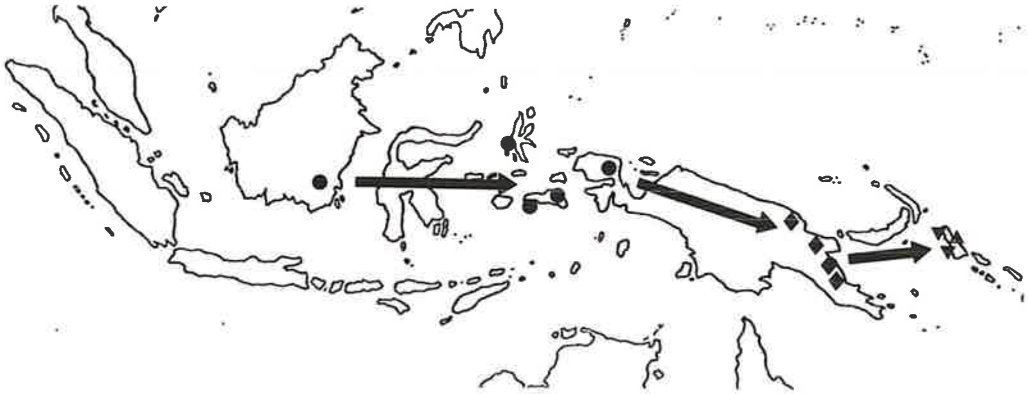

Fig. 27. Possible speciation course of the species in sect. Blephalopetalum. ●, *P. mastersianum.* ◆, *P. violascens.* ▼, *P. wentworthianum.* ▲, *P. bougainvilleanum.*

chromosome numbers. The chromosome number of *P. mastersianum* is the smallest (2n=36), *P. violascens* (=*P. papuanum*) 2n=38, *P. bougainvilleanum* 2n=40, and that of *P. wentworthianum* is 2n=42. The karyotypes of these four species are similar to each other and the relations between them are showed in Fig. 26. The loss of minute dots on petal surface and the widening of lateral petals seem to be closely associating with the increasing of chromosome numbers. On the other hand, the species with the smallest chromosome number and with the narrowest lateral petals (*P. mastersianum*) is distributed in the most west part (East Borneo) within sect. Blephalopetalum, and the distributional ranges are shifting eastward with karyotype changing (differentiation). It seems to suggest that the speciation within this section has happened through the divergence of plants to the new habitats from West Irian to New Guinea and Bougainville Islands. Thus the phyletic line of karyotype is closely correlated not only with the differentiation of floral morphologies but also with the shifting of distributional ranges of each species, and these conditions of various characters are apparently indicate that sect. Blephalopetalum is a well recognizable taxon as a natural species assemblage (Fig. 27).

With regard to the phylogenetic relation with the other sections, this section seems to have evolved in parallel by the increasing of chromosome numbers. But the indistinctness of longitudinal stripes of upper sepal and the narrow spathulate lateral petals of *P. mastersianum* are similar to those of *P. bullenianum* in appearance, and both taxa are considered to be rather closely related each other than to the other sections.

Key to species of sect. Blephalopetalum

1\. Lateral petals horizontally spreading, narrowest at base, gradually widened toward apex; vertical stripe on upper sepal indistinct; chromosome number 2n=36——*P. mastersianum*

1\. Lateral petals more or less declvitous, almost same width from base to apex; vertical stripes on upper sepal distinct——————2

2. Lateral petals hardly arched, margin strongly undulate; chromosome number $2n=40$ ——— *P. wentworthianum*
2. Lateral petals more or less arched, margin hardly undulate ——— 3
3. Lateral petals tinged with deep purple; upper sepal tinged with pale purple; staminode semi-curcular; chromosome number $2n=38$ ——— *P. violascens*
3. Lateral petals tinged with pale greenish purple; upper sepal tinged with pale green; staminode semi-lunate; chromosome number $2n=40$ ——— *P. bougainvilleanum*

* ***Paphiopedilum mastersianum*** (Reichb. f.) Stein, Orchideenbuch 477 (1892).
  – *Cypripedium mastersianum* Reichb. f., Gard. Chron. 2: 102 (1879).
* ***Paphiopedilum violascens*** Schltr., Feddes Repert. Beih. 1: 2–3 (1911).
  – *Cypripedium papuanum* Ridley, Gard. Chron. ser. 3, lviii: 131 (1915), *syn. nov.*
  – *Paphiopedilum papuanum* (Ridl.) L. O. Williams, Bot. Mus. Leafl. Harvard Univ. 12: 149 (1946).
* ***Paphiopedilum bougainvilleanum*** Fowlie, Orch. Dig. 35: 122 (1971).
* ***Paphiopedilum wentworthianum*** Schoser et Fowlie, Orch. Dig. 32: 282–285 (1968).

Sect. **Punctatum** Karasawa et Saito, *sect. nov.*

Sect. Blephalopetali similis, sed differt petalis punctatis margine superioribus clavatis.

Type species: *Paphiopedilum tonsum* (Reichb. f.) Stein

Sect. Punctatum is rather similar to sect. Blephalopetalum in the linear-oblong petals, the absence of the cilia on petal margin and the relatively indistinct longitudinal stripes on upper sepal, but it is clearly distinguished from Blephalopetalum in the presence of large spots at middle portion of petals. While the large spots on petals is a common feature with subsect. Barbata of sect. Barbata, sect. Planipetalum and sect. Sigmatopetalum. Those taxa are much different from sect. Punctatum in the presence of large cilia on petal margin and the distinctness of longitudinal stripes of upper sepal. Thus sect. Punctatum exhibits intermediate features between sect. Blephalopetalum and sect. Barbata, but there seems to be no direct relationships with two sections. Though the karyotype of *P. tonsum* ($2n=20V+12I=32$) is common with those of *P. callosum* and *P. ciliolare* of sect. Barbata and seems to retain rather primitive karyotype within subgen. Sigmatopetalum, there also seems to be no direct relationships between them.

* ***Paphiopedilum tonsum*** (Reichb. f.) Stein, Orchideenbuch 488 (1892).
  – *Cypripedium tonsum* Reichchb. f., Gard. Chron. 2: 262 (1888).

Sect. **Barbata** Kranzl., Orchidacearum Genera et Species, 53–73 (1901).

Type species: *Paphiopedilum barbatum* (Lindl.) Pfitz.,
– Sect. *Phacopetalum* Pfitz., Engl. Pflanzenreich 4(50): 87–94 (1903).

Sect. Barbata is the largest section in the genus *Paphiopedilum* including more than 12 species. There are many intra- and interspecific variations of morphological characters, especially in floral characters, and there have been reported some ambiguous species. This makes the taxonomy of this section very difficult. In spite of the vast variations in many morphological characters, sect. Barbata is well distinguished from the other sections by the following combination of the characteristics: 1) longitudinal stripes of upper sepal distinct, 2) cilia on lateral petal margin well developed, 3) lateral petals linear-oblong, more or less twisted in the apical portion, 4) staminode semi-orbiculate or/to oblong, and 5) under surface of leaves pale green throughout, hardly tinged with purple pigments. As closely reported by Karasawa (1979), karyotype in this section is very variable in chromosome numbers as well as in detailed structure of chromosomes, and there seems to be chromosome increasing series within this section.

The species of sect. Barbata are classified into three groups based mainly on the differences of floral characters. And there are chromosome increasing series in each group. This suggest that each species group is a natural taxon, though the interrelationships between those subsections are still in doubt. Three subsections in sect. Barbata are subsect. Barbata, Loripetalum and Chloroneura (Fig. 28).

Fig. 28. Distributions of the subsection in sect. Barbata.
●, subsect. Barbata. ■, subsect. Loripetallum. ▲, subsect. Chloroneura.

Key to subsections of sect. Barbata

1. Upper sepal well developed, large, more or less rounded, apical portion not incurved, but gently recurved: large, deep purple, slightly swollen blotches on lateral petal margin; blotches with long, blackish cilia ———— subsect. Barbata
1. Upper sepal ovate, sharply acute, and strongly carinate at apex; blotches hardly present on lateral petal margin ———— 2
2. Lateral petal margin with black, regularly arranged long cilia throughout: staminodes

semi-orbiculate, surface densely covered with short cilia ———— subsect. Loripetalum

2. Lateral petal margin ciliate only from the swollen blotches, or faintly hairly: staminode almost smooth on surface ———— subsect. Chloroneura

Subsect. **Barbata**

Type species: *Paphiopedilum barbatum* (Lindl.) Pfitz.

Subsect. Barbata is well characterized by the following characters; 1) lateral petals with some warty, large ciliate spots at margin, 2) upper sepal large, nearly rounded, widest above middle, and 3) margin of upper sepal gently recurved in upper half. Within this subsection, there seems to be a increasing series of warty, ciliate spots on lateral petals: warty spots are restricted to upper side in *P. callosum* (2n=32), and *P. barbatum* (2n=38), they are on both sides in *P. lawrenceanum* (2n=36) and *P. hennisianum* (2n=36) and scattered on whole surface of lateral petals in *P. argus* (2n=38). Increasing tendency of warty spots seems to be related with the differentiation of shape and size of upper sepal. The differentiation of external morphological characters do not necessarily associate with the chromosome differentiation, subsect. Barbata seems to be inferable that it is a natural taxon and has evolved through the differentiation of external morphological characters and probably with that of karyotype.

Key to species of subsect. Barbata

1. Blotches on lateral petals restricted to upper margin ———— 2
1. Blotches on lateral petals observed on both sides of margin ———— 3
2. Lateral petals almost horizontally spreading or slightly downwards; upper sepal 3–4. 5 cm in width; chromosome number 2n=38 ———— *P. barbatum*
2. Lateral petals strongly declivitous; upper sepal 5–6 cm in width; chromosome number 2n=32 ———— *P. callosum*
3. Lateral petals declivitous, blotches scattered on whole surface; chromosome number 2n=38 ———— *P. argus*
3. Lateral petals horizontally spreading, blotches restricted to marginal portion ———— 4
4. Vertical stripes on upper sepal greenish below, dark purple above middle; staminode wider than long, margin not recurved; chromosome number 2n=36=16V + 20I ———— *P. lawrenceanum*
4. Vertical stripes greenish throughout; staminode almost same in both width and length; chromosome number 2n=36=18V + 18I ———— *P. hennisianum*

* ***Paphiopedilum argus*** (Reichb. f) Pfitz., Engl. Bot. Jahrb. 19: 40 (1894)
 – *Cypripedium argus* Reichb. f., Gard. Chron., 608 (1873).

* ***Paphiopedilum callosum*** (Reichb. f.). Stein, Orchideenbuch 457 (1892)
 – *Cypripedium callosum* Reichb. f., Gard. Chron. 2: 326 (1882).

* ***Paphiopedilum barbatum*** Lindl., Bot. Reg., Misc. 53 (1841).

* ***Paphiopedilum lawrenceanum*** (Reichb. f.) Pfitz., Engl. Bot. Jahrb. 19: 40 (1894).
– *Cypripedium lawrenceanum* Reichb. f., Gard. Chron. 2: 748 (1878) – *Paphiopedilum barbatum* (Lindl.) Pfitz. subsp. *lawrenceanum* (Rchb. f.) Wood, Orch. Review 84: 352 (1976)

* ***Paphiopedilum hennisianum*** (Wood) Fowl. Orch. Digest 41: 60 (1977).
– *Paphiopedilum barbatum* (Lindl.) Pfitz. subsp. *Lawrenceanum* (Reichb. f.) Pfitz. var. *hennisianum* Wood, Orch. Review 84: 352 (1976).

Subsect. **Loripetalum** Karasawa et Saito, *subsect. nov.*

Subsect. Barbatae similis, sed differt sepalum parvis ovatis, petalis falcatis loriformibus margine ciliis longioribus nigris non punctatis.

Type species: *Paphiopedilum ciliolare* (Reichb. f.) Stein

Subsect. Loripetalum is somewhat similar to some species of subsect. Barbata (*P. argus* and *P. hennisianum*), but it is well characterized by the following characters: 1) upper sepal relatively small, ovate, 2) apical margin of upper sepal slightly incurved and forming a sharply pointed apex, 3) large, warty ciliate spots absent on marginal portion of lateral petals, 4) long, black cilia uniformly and regularly protruded from lateral petal margin, and 5) staminode semiorbiculate and covered with minute hairs.

Within this subsection, *P. dayanum* is a distinct species and well distinguished from the rest by the detailed features of lateral petals. The 3 species, as *P. ciliolare* (2n=32), *P. curtisii* (2n=36) and *P. superbiens* (2n=38) are, on the contrary, very closely similar and hardly distinguishable to each other, but the chromosome numbers are apparently different to each other. All three species had been described by Reichenbach fil. (*P. superbiens* 1855, *P. ciliolare* 1882, *P. curtisii* 1883) as the species of *Cypripedium*, although we could not certify the karyotypes of each type plants, typical plants of each species are showing actually the different karyotypes. We think that these 3 species are doubtlessly forming a species complex, and *P. ciliolare* and *P. superbiens* are the extreme forms of this species complex.

Key to species of subsect. Loripetalum

1. Lateral petals without blotches, linear lanceolate: chromosome number 2n=36 ———— *P. dayanum*
1. Lateral petals lanceolate, with minute blotches ———— 2
2. Apical portion of lateral petals hardly sinuate, not blotched: chromosome number 2n=32 ———— *P. ciliolare*
2. Apical portion of lateral petals more or less sinuate, finely blotched at middle portion: chromosome number 2n=38 (2n=36 in P. curtisii) ———— *P. superbiens*

* ***Paphiopedilum dayanum*** (Reichb. f.) Stein, Orchideenbuch, 464 (1892)
– *Cypripedium dayanum* Reichb. f., Bot. Zeit. 20: 214 (1862).

* ***Paphiopedilum ciliolare*** (Reichb. f.) Stein, Orchideenbuch 462 (1892).
– *Cypripedium ciliolare* Reichb. f., Gard. Chron. 2: 488 (1882).

* ***Paphiopedilum superbiens*** (Reichb. f.) Stein, Orchideenbuch, 487 (1892).
– *Cypripedium superbiens* Reichb. f., Bonplandia 3: 227 (1855). – *Paphiopedilum curtisii* (Reichb. f.) Stein, Orchideenbuch, 464 (1892). – *Cypripedium curtisii* Reichb. f., Gard. Chron. 20: 8 (1883).

Subsect. **Chloroneura** Hall., Ann. Jard. Buitenzorg 14: 36 (1896).

Type species: *Paphiopedilum javanicum* (Reinw.) Pfitz.

Subsect. Chloroneura is clearly distinguished from the rest subsections by the entirely smooth surface of staminode, and the reddish purple apical portion of lateral petals. Although the species of this subsection are easily distinguishable from each other, the variations in characters are not wide in both of external morphology and chromosome morphology. And there seems to be no recognizable phylogenetic tendency of characters in this subsection. Moreover, the phyletic relation to the rest taxa is also detectable, and it seems to have evolved independently from the ancestral stock of subgen. Sigmatopetalum and to be the most actively diversifying species assemblage.

Key to species of subsect. Chloroneura

1\. Upper sepal greenish, with deep green longitudinal stripes, apical portion more or less incurved, forming a sharply pointed apex: staminode semi-circular —— 2.

1\. Upper sepal whitish, with deep purple longitudinal stripes, apical portion hardly incurved, broadly acute at apex: staminode oblong-rhomboid —— 3

2\. Lateral petals almost horizontally spreading; staminode slightly recurved backward in marginal portion, faintly protruded at middle: chromosome number 2n=40 —— *P. virens*

2\. Lateral petals slightly declivitous: staminode slightly curving forward in marginal portion, more or less hollowed at middle: chromosome number 2n=38 —— *P. javanicum*

3\. Lip almost same width at middle and mouth, middle portion longitudinally keeled at mouth: lateral petals narrow-oblong, almost rounded or broadly acute at apex: basal portion of upper sepal often tinged with pale reddish purple: chromosome number 2n=36 —— *P. acmodontum*

3\. Lip much widened at mouth, hardly carinate at middle: lateral petals linear oblong, sharply acute at apex: upper sepal whitish throughout: chromosome number 2n=40 —— *P. urbanianum*

* ***Paphiopedilum acmodontum*** Wood, Orch. Rev., 84: 350–352 (1976).

* ***Paphiopedilum javanicum*** (Reinw.) Pfitz., Engl. Bot. Jahrb. 19: 40. (1894).
– *Cypripedium javanicum* Reinw., Blume, Cat. Gew Buitenz. 98 (1823).

* ***Paphiopedilum urbanianum*** Fowl., Orch. Dig. 45 (4): 131–134 (1981).

* ***Paphiopedilum virens*** (Reichb. f.) Pfitz., Engl. Bot. Jahrb. 19: 44 (1894).
– *Cypripedium virens* Reichb. f., Bot. Zeit. 19: 44 (1896).

Sect. **Planipetalum** Karasawa et Saito, *sect. nov.*

Sect. Barbatae similis, sed differt petalis anguste ellipticis transversaliter planis.

Type species: *Paphiopedilum sukhakulii* Schoser et Senghas

Sect. Planipetalum is very similar to sect. Barbata in the distinct longitudinal stripes on dorsal sepal and the occurrence of long cilia on laterl petal margin, but it is different in the narrow oblong, transversely spreading plain lateral petals and in the crescent-shaped staminode. Among these features, the narrow oblong, plain lateral petals is considered to be the derived one. Karyotypes of *P. purpuratum* and *P. sukhakulii* are also considered to be showing the derived features as indicated by Karasawa (1979). Distribution ranges of both species are just limited to South of China and North of Hong Kong. These features of both species are considered to suggest that both species have been diversified in relatively recent time, but the transitional forms from the ancestral stock are missing. Sect. Planipetalum are considered to be a well specialized, natural species assemblage.

Key to species of sect. Planipetalum

1. Lateral petals long, sharply acute at apex, pale greenish, almost uniformly spotted with deep blackish-purple dots: dorsal sepal ovoid, narrowly acuminate at apex: longitudinal stripes on dorsal sepal green ——— *P. sukhaklii*
1. Lateral petals short, bluntly acute at apex, purple, finely spotted at basal portion with minute blackish points: dorsal sepal rounded, usually strongly recurved in lower half, broadly acuminate at apex: longitudinal stripes on dorsal sepal purplish —— *P. purpuratum*

* ***Paphiopedilum purpuratum*** (Lindl.) Pfitz., Engl. Bot. Jahrb. 19: 41 (1894).
– *Cypripedium purpuratum* Lindl., Bot. Reg. 33, t. 1991, (1837).
* ***Paphiopedilum sukhakulii*** Schoser et Senghas, Die Orchidee, 16: 244 (1965).

Sect. **Sigmatopetalum**

Type species: *Paphiopedilum venustum* (Wall.) Pfitz.

Sect. Sigmatopetalum seems to be closely related to sect. Barbata and similar in the following characteristics: 1) lateral petals narrow oblong, slightly widened toward apex, more or less twisted at apex, 2) staminode semi-circular to/or oblong, 3) dosral sepal distinctly striped with green longitudinal stripes, 4) long cilia on lateral petal margin, and 5) large, dark purplish dots sparsely scattered on lateral petals. But sect. Sigmatopetalum is clearly distinguished from the other sections by 1) deep purplish green, tessellated leaves and 2) the grotesquely veined, yellowish brown lip. Another noteworthy character of this species is its distribution area: *P. venustum* is known from the northern most area within this subgenus (Nepal, Bangladesh, Assam, and East India). Except the dark purplish, tessellated leaves, *P. venustum* is similar to those of the species of sect. Barbata in sepal and petal morphology, and the species is considered to be one of the specialized species through the adaptation to temperate region accompanying with the differentiation of karyotype and in the detailed features of leaves and flowers.

* ***Paphiopedilum venustum*** (Wall.) Pfitz., Engl. Bot. Jahrb. 19: 41 (1894).
– *Cypripedium venustum* Wall., Bot. Mag. t. 2129.

6. Subgenus **Cochlopetalum** (Hall.) Karasawa et Saito, *stat. nov.*

Type species: *Paphiopedilum victoria-regina* (Sand.) Wood

– Subgen. *Chromatoneura* Hall. sect. *Cochlopetalum* Hall., Ann. Jard. Buitenzorg 14: 44 (1896). – Subgen. *Otopedilum* Pfitz. sect. *Polyantha* Pfitz., Engl. Bot. Jahrb. 19: 42 (1894). – Subgen. *Polyantha* (Pfitz.) Brieg. sect. *Cochlopetalum* Hall., Die Orchideen 174 (1971).

Subgen. Cochlopetalum has long been treated as a member of subgen. Polyantha (*sensu lato*) because of the pluri-flowered racemes, but it is clearly different in the following characteristics: 1) flowers spreading out separately, 2) leaves greyish green throughout or faintly tessellated, 3) chromosome complement 2n=30–36 (37)=25V, and 4) lateral petals linear, strongly twisted, vertically spreading, irregularly and roughly blotched, and regularly ciliate at margin. Though there are many variations, the morphological features of this subgenus are rather uniform and forming a coherent species assemblage. The chromosome complement of this subgenus 2n=30–36 (37) is considered to be derived by the loss of a pair of I-chromosomes as indicated by Karasawa (1979). One of the important evidence which indicates the independency of this subgenus is that there is a phyletic line of chromosome increasing (2n=30 – 32 – 34 – 36 or 37) accompanying with the differentiation of some floral characters (color patterns of dorsal sepal and lateral petals), and the chromosome increasing series is nothing less than the speciation series within this subgenus.

Fig. 29. Distributions of the species in subgenus Cochlopetalum.
●, *P. chamberlainianum.* ■, *P. glaucophyllum.* ▲, *P. liemianum.* ▼, *P. victoria-regina*

Phytogeographically, subgen. Cochlopetalum is restricted to Java and Sumatra (Fig. 29), and the distribution ranges of each species in this subgenus are quite limited and much smaller than those of the most species of *Paphiopedilum*. In spite of the fact that these species are not unusual but commonly found in those areas, the small ranges of all species seem to suggest that these species have evolved in relatively recent time and not yet shifted nor diversified. Addition to the occurrence of many interspecific hybrids (Karasawa 1979), there are many intermediate plants between the different species and are also vast intraspecific variations in many morphological characters, especially in floral ones. These conditions of this taxon seem to suggest that Cochlopetalum is genetically very active species assemblage, and it is still under diverging. Especially, the close similarity in most floral characters of *P. victoria-regina* which has the most primitive type of pluri-flowered racemes and linear, regularly ciliate petals of Cochlopetalum seems to suggest the close relationship with Polyantha in appearance. The close similarity in most floral characters of *P. victoria-regina,* which has the most primitive karyotype within subgen. Cochlopetalum, to *P. lowii* of sect. Polyantha does not suggest the direct phylogenetic relationship between the two species. The separate spreading of flowers and the greyish green leaves as well as the 2n=25V chromosome complement indicate the great difference in phylogenetic relationships between the two subgenera. These characteristics of Cochlopetalum are considered to be relatively derived features than those of subgen. Polyantha as discussed before (see p. 6, 12, 26), and Cochlopetalum is considered to be derived from Polyantha (probably lost ancestral stock allied to *P. lowii*) through the differentiation of flowering mode, detailed morphology of leaves and floral characters as well as the karyotype differentiation in relatively recent time.

Key to species of subgen. Cochlopetalum

1. Lateral petals purplish green, strongly undulate at margin, not blotched: lip without fine, deep purple blotches: chromosome number 2n=30 —— *P. victoria-regina*
1. Lateral petals roughly marbled with dark purplish portions and white or creamy white portions: lip more or less spotted with fine, dark purplish spots —— 2
2. Leaf margin ciliate from base to apex: vertical stripes of dorsal sepal hardly recognizable: chromosome number 2n=32 —— *P. liemianum*
2. Leaf margin ciliate only in the basal portion: vertical stripes of dorsal sepal well recognizable —— 3
3. Leaf surface grayish green: leaves thin, ca. 0.47 mm thick in cross section: dorsal sepal more or less tinged with brown throughout: chromosome number 2n=36 (or 37) —— *P. glaucophyllum*
3. Leaf surface green throughout: leaves thick, ca. 0.8–0.9 mm thick in cross section: vertical stripes on dorsal sepal much thicker and deeper in color, deep brown to almost black: chromosome number 2n=34 —— *P. chamberlainianum*

* ***Paphiopedilum victoria-regina*** (Sand.) Wood, Orch. Rev. 84: 134 (1976).

– *Cypripedium victoria-regina* Sand., Gard. Chron. ser. 3, 11: 194 (1892). – *Cypripe-*

dium victoria-mariae Sand. ex T. Mast. nom. illeg., Gard. Chron. ser. 3, 13: 580 (1893). – *Cypripedium chamberlainianum* forma *victoria-mariae* (Sand. ex Mast.) Rolf., nom. illeg., Orch. Rev. 1: 188 (1893).

* ***Paphiopedilum liemianum*** (Fowlie) Karasawa et Saito, *stat. nov.*

– *Paphiopedilum chamberlainianum* (Sand.) Stein subsp. *liemiana* Fowlie, Orch. Dig. 33: 55 (1971). – *Paphiopedilum victoria-regina* (Sand.) Wood subsp. *liemianum* (Fowlie) Wood, Orch, Rev. 84: 138 (1976).

* ______var. ***primulinum*** (Wood et Taylor) Karasawa et Saito, *stat. nov.*,

– *Paphiopedilum primulinum* Wood et Taylor, Orch. Rev. 81: 955 (1973). –*Paphiopedilum victoria-regina* (Sand.) Wood subsp. *primulinum* (Wood et Taylor) Wood, Orch. Rev. 84: 139 (1976). –*Paphiopedilum chamberlainianum* subsp. *liemianum* forma *primulinum* Fowlie, Orch. Dig. 37: 104 (1973).

* ***Paphiopedilum chamberlainianum*** (Sand.) Stein, Orchideenbuch: 461 (1892).

– *Cypripedium chamberlainianum* Sand., Gard. Chron. ser. 3, 11: 194 (1892). – *Paphiopedilum victoria-regina* (Sand.) Wood subsp. *chamberlainianum* (Sand.) Wood, Orch. Rev. 84: 135 (1976).

* ***Paphiopedilum glaucophyllum*** Smith, Bull. de L'Inst. Bot. Buitenz., 7: 1 (1900).

– *Cypripedium glaucophyllum* (Smith) Mast., Gard. Chron. ser. 3, 34: 405 (1903).

– *Paphiopedilum victoria-regina* (Sand.) Wood subsp. *glaucophyllum* (Smith) Wood, Orch. Rev. 84: 137 (1976).

* _______ var. ***moquetteanum*** Smith, Teysmannia 17: 31 (1906).

– *Paphiopedilum victoria-regina* (Sand.) Wood subsp. *glaucophyllum* (Smith) Wood var. *moquetteanum* (Smith) Wood, Orch. Rev. 84: 137 (1976).

Synopsis

Subgenus PARVISEPALUM Karasawa et Saito, *subgen. nov.*
    P. armeniacum Chen et Liu
    P. delenatii Guill.
    P. micranthum Tang et Wang
Subgenus BRACHYPETALUM Hallier
    P. bellatulum (Rchb. f.) Stein
    P. concolor (Batem.) Pfitz.
    P. leucochilum (Rolfe) Fowl.
    P. niveum (Rchb. f.) Stein
Subgenus POLYANTHA (Pfitz.) Brieger
  Sect. MASTIGOPETALUM Hallier
    P. elliottianum (O'Brien) Stein
    P. philippinense (Rchb. f.) Stein
    P. praestans (Rchb. f.) Pfitz.
    P. randsii Fowl.

P. rothschildianum (Rchb. f.) Stein
P. sanderianum (Rchb. f.) Stein
P. stonei (Hook.) Stein
Sect. POLYANTHA
P. haynaldianum (Rchb. f.) Stein
P. lowii (Lindl.) Stein
Sect. MYSTROPETALUM Pfitz.
P. parishii (Rchb. f.) Stein
P. p. var. *dianthum* (Tang et Wang) Karasawa et Saito, *stat. nov.*
Subgenus PAPHIOPEDILUM
Sect. STICTOPETALUM Hallier
P. hirsutissimum (Lindl. et Hook.) Stein
P. h. var. *esquirolei* (Schltr.) Karasawa et Saito, *stat. nov.*
Sect. PAPHIOPEDILUM
P. charlesworthii (Rolfe) Pfitz.
P. exul (Ridl.) Rolfe
P. insigne (Lindl.) Pfitz.
P. villosum (Lindl.) Stein
Sect. THIOPETALUM Hallier
P. druryi (Beddome) Stein
P. spicerianum (Rchb. f.) Pfitz.
Sect. CERATOPETALUM Hallier
P. fairrieanum (Lindl.) Stein
Subgenus SIGMATOPETALUM Hallier
Sect. SPATHOPETALUM Pfitz.
Subsect. MACRONODIUM Karasawa et Saito, *subsect. nov.*
P. hookerae (Rchb. f.) Stein
Subsect. SPATHOPETALUM
P. appletonianum (Gower) Rolfe
P. bullenianum (Rchb. f.) Pfitz.
P. celebesensis Fowl. et Birk
Sect. BLEPHALOPETALUM Pfitz.
P. bougainvilleanum Fowl.
P. mastersianum (Rchb. f.) Stein
P. violascens Schltr.
P. wentworthianum Schoser ex Fowl.
Sect. PUNCTATUM Karasawa et Saito, *sect. nov.*
P. tonsum (Rchb. f.) Stein
Sect. BARBATA Krzl.
Subsect. BARBATA
P. argus (Rchb. f.) Stein
P. barbatum (Lindl.) Pfitz.

P. callosum (Rchb. f.) Stein
P. hennisianum (Wood) Fowl.
P. lawrenceanum (Rchb. f.) Pfitz.
Subsect. LORIPETALUM Karasawa et Saito, *subsect. nov.*
P. dayanum (Rchb. f.) Stein
P. ciliolare (Rchb. f.) Stein
P. superbiens (Rchb. f.) Stein
Subsect. CHLORONEURA Hallier
P. acmodontum Wood
P. javanicum (Reinw.) Pfitz.
P. urbanianum Fowl.
P. virens (Rchb. f.) Pfitz.
Sect. PLANIPETALUM Karasawa et Saito, *sect. nov.*
P. purpuratum (Lindl.) Stein
P. sukhakulii Schoser et Senghas
Sect. SIGMATOPETALUM
P. venustum (Wall.) Pfitz.
Subgenus COCHLOPETALUM (Hallier) Karasawa et Saito, *subgen. nov.*
P. victoria-regina (Sander) Wood
P. liemianum (Fowl.) Karasawa et Saito, *stat. nov.*
P. l. var. *primulinum* (Wood et Tayl.) Karasawa et Saito, *stat. nov.*
P. chamberlainianum (O'Brien) Stein
P. glaucophyllum (Smith) Pfitz.
P. g. var. *moquetteanum* Smith

Species considered to be hybrids

Based on the close observations of external morphology and karyotypes, we consider that the following 14 species are possibly natural hybrids.

P. ang-thong Fowl.
P. annamense Guill.
P. bunditianum Hort.
P. directum (Rchb. f.) Pfitz.
P. gratrixianum (Sander) Buill.
P. godefroyae (Godefr.-Lebeuf.) Stein
P. jogjae Hort.
P. pradhanii Pradhan
P. robinsonii (Ridl.) Ridl.
P. siamense Rolfe
P. sublaeve (Rchb. f.) Fowl.
P. wardii Summerhayes
P. yapianum Hort.
P. zickianum Shoser

Species untreated

P. affine De Wild
P. amboinensis, nomen nudum
P. barbigerum Tang & Wang
P. bodegomii Hort.
P. fowliei Birk
P. gardineri (Guill.) Pfitz.
P. kinballianum Linden
P. neo-guineense, nomen nudum
P. nigritum Rchb. f
P. pardinum Pfitz.
P. petri Rchb. f.
P. purpurascens Fowl.
P. robinsonii (Ridl.) Ridl.
P. schmidtianum Krzl.
P. thailandense Fowl.
P. wilhelminiae L. Wms.

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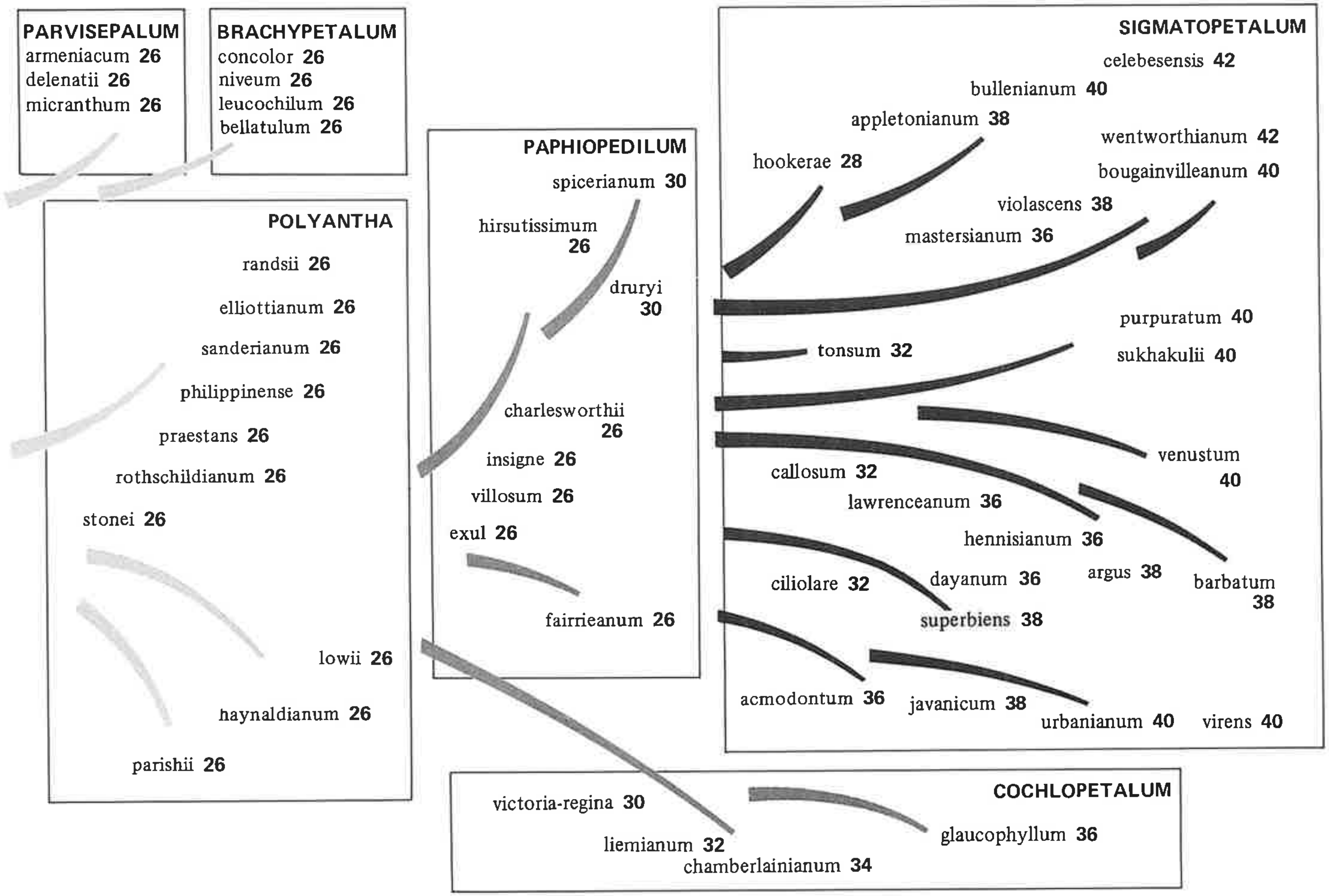

Fig. 30. Proposed phyletic arrangement of *Paphiopedilum*.

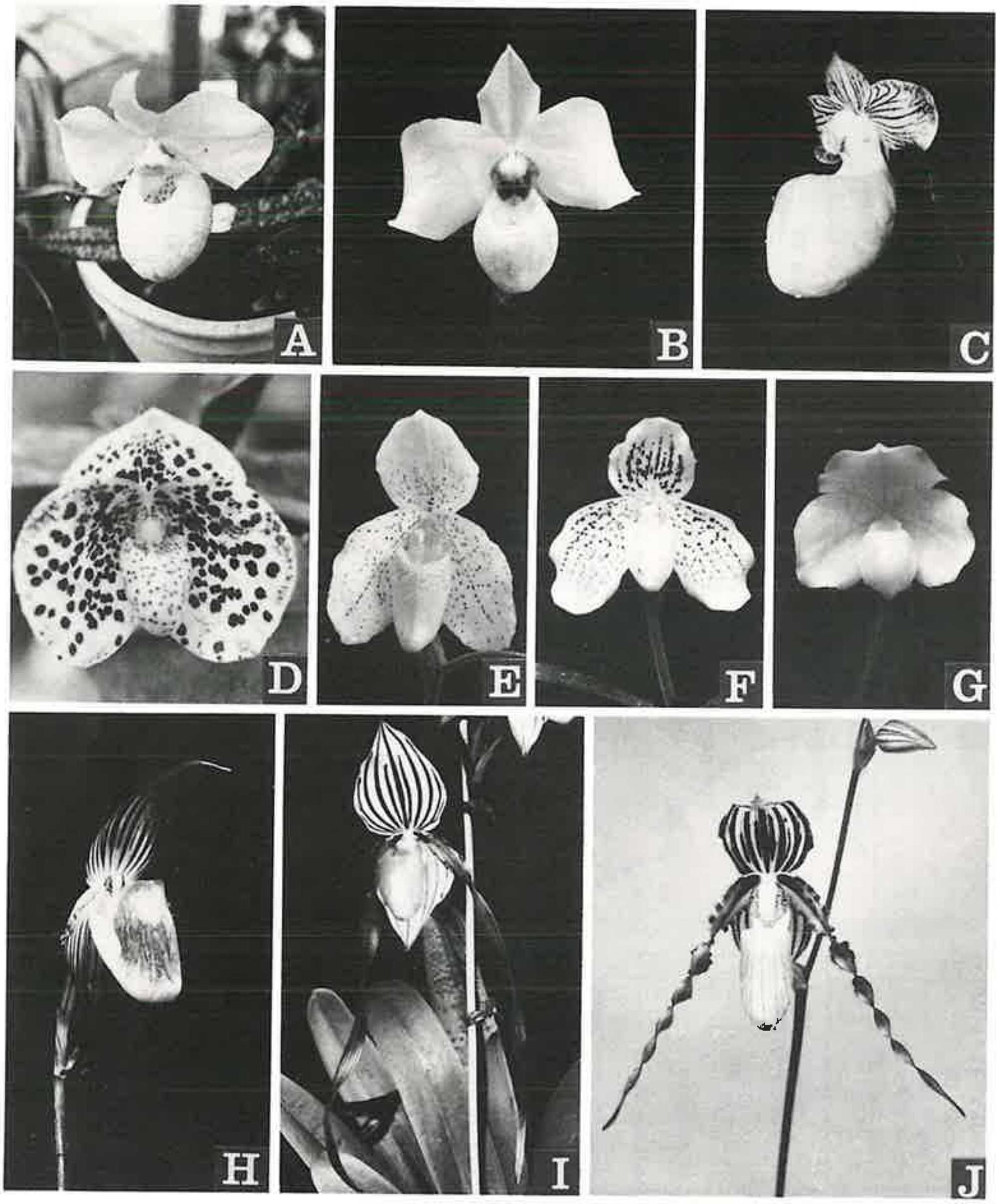

Fig. 31. Flowers of *Paphiopedilum*.
A, *P. armeniacum* (photo by Mr. Satoshi Kimura). B, *P. delenatii*. C, *P. micranthum* (photo by Mr. Tamotsu Hashimoto). D, *P. bellatulum*. E, *P. concolor*. F, *P. leucochilum*. G, *P. niveum*. H, *P. elliottianum*. I, *P. philippinense*. J, *P. praestans*. × 0.4.

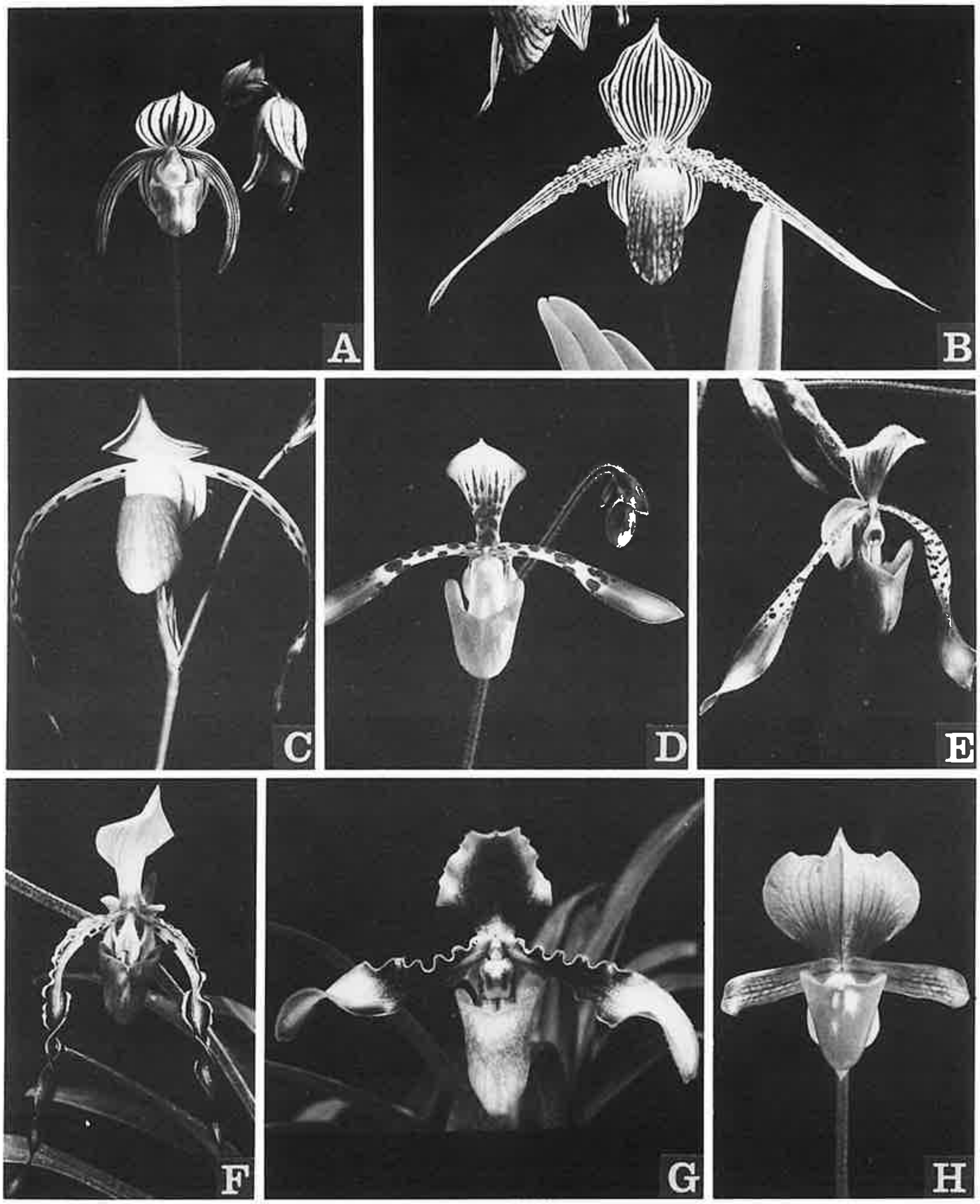

Fig. 32. Flowers of *Paphiopedilum*.
A, *P. randsii.* B, *P. rothschildianum.* C, *P. stonei.* D, *P. haynaldianum.* E, *P. lowii.* F, *P. parishii.* G, *P. hirsutissimum.* H, *P. charlesworthii.* x 0.4.

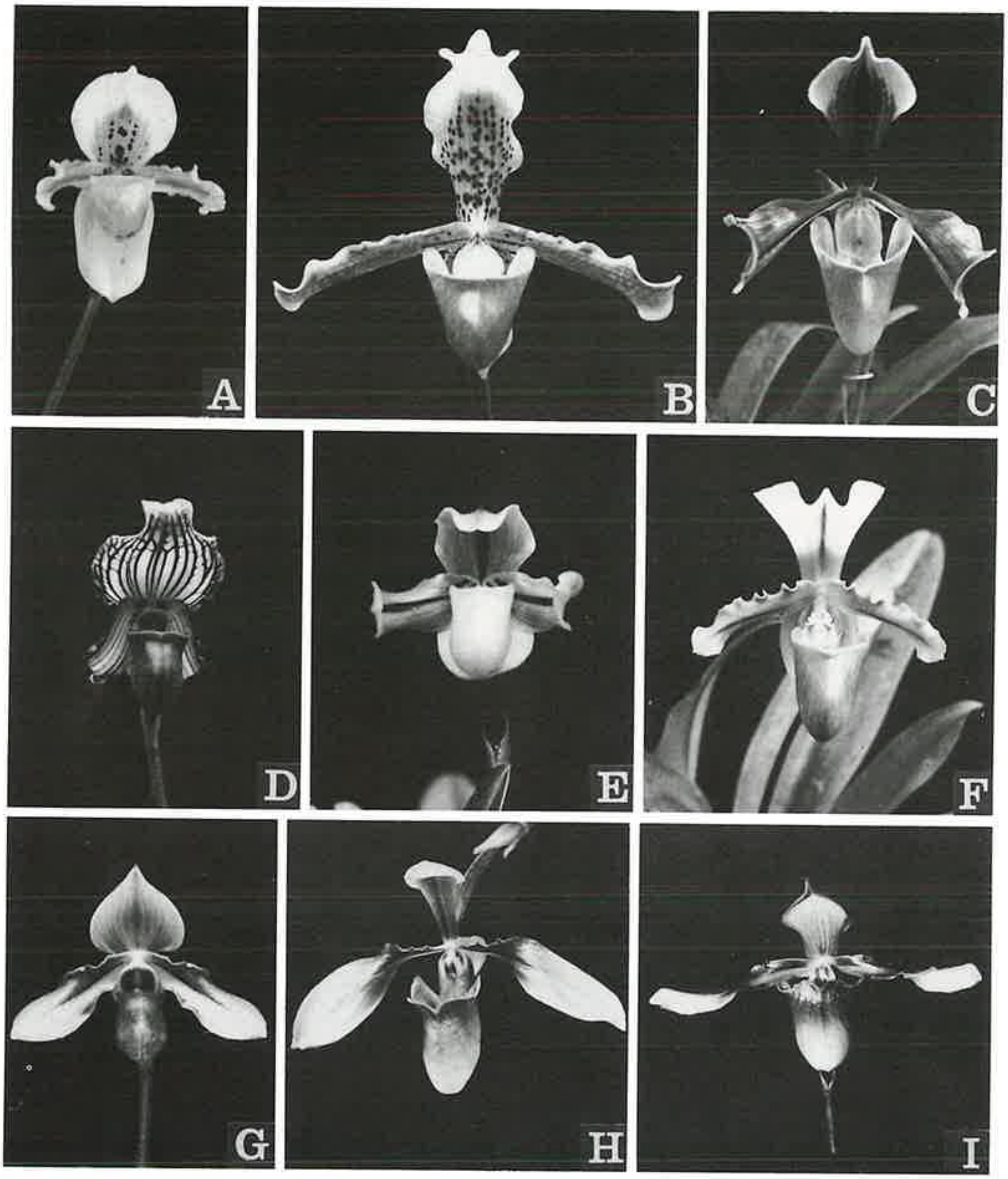

Fig. 33. Flowers of *Paphiopedilum*.
A, *P. exul.* B, *P. insigne.* C, *P. villosum.* D, *P. fairrieanum.* E, *P. druryi.* F, *P. spicerianum.* G, *P. hookerae.* H, *P. appletonianum.* I, *P. bullenianum.* × 0.4.

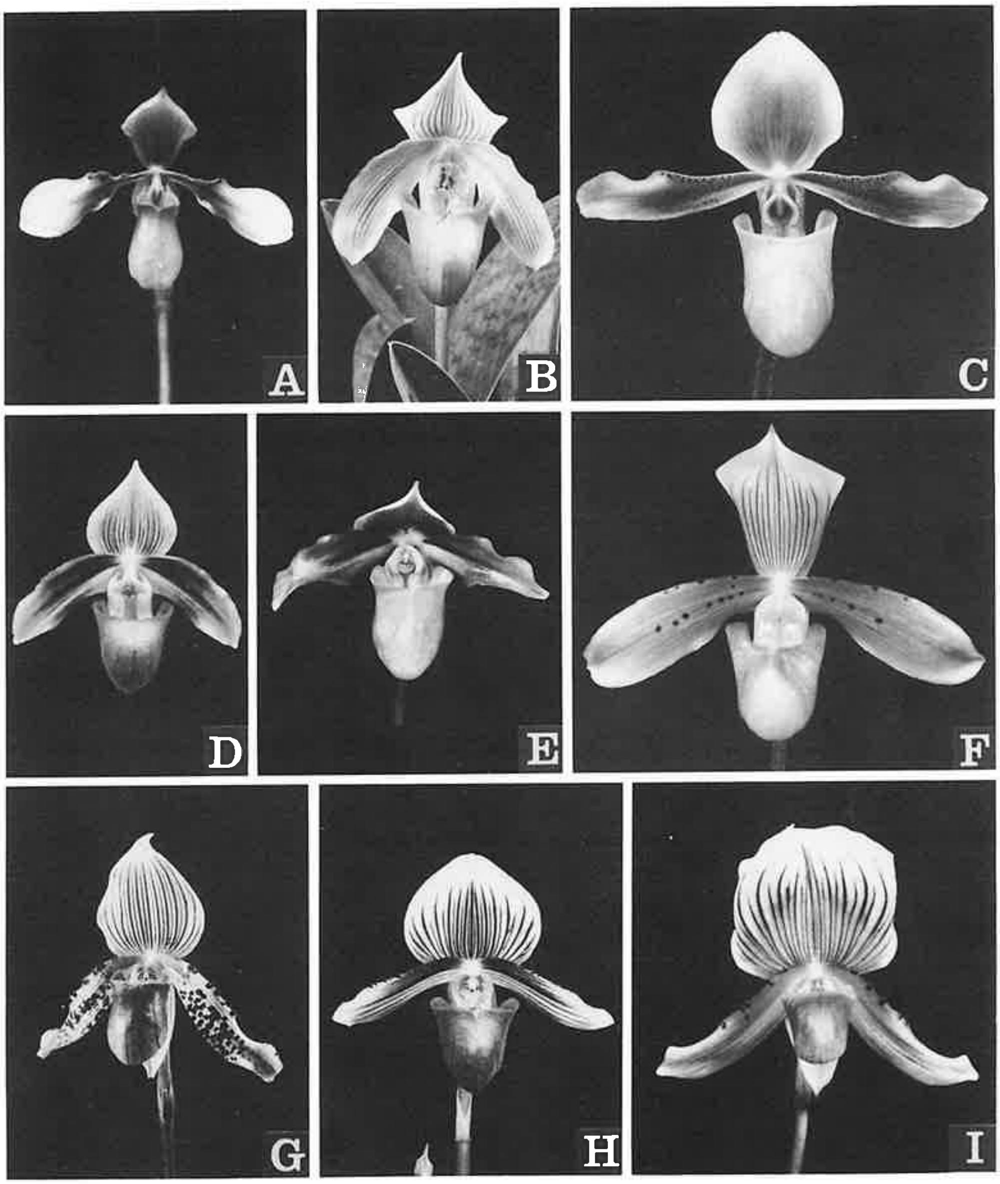

Fig. 34. Flowers of *Paphiopedilum*.
A, *P. celebesensis*. B, *P. bougainvilleanum*. C, *P. mastersianum*. D, *P. violascens*. E, *P. wentworthianum*. F, *P. tonsum*. G, *P. argus*. H, *P. barbatum*. I, *P. callosum*. × 0.4.

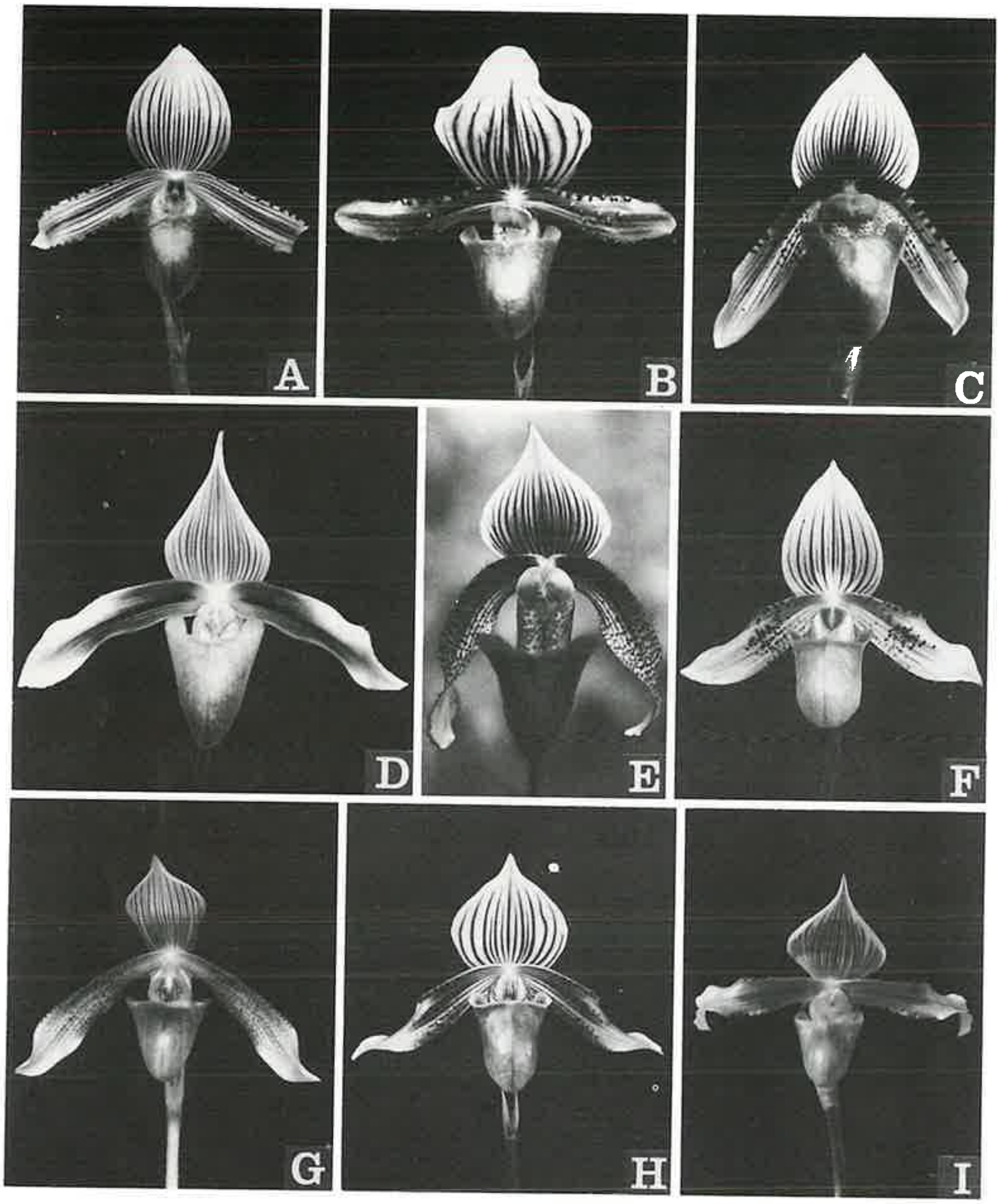

Fig. 35. Flowers of *Paphiopedilum*.
A, *P. hennisianum*. B, *P. lawrenceanum*. C, *P. ciliolare*. D, *P. dayanum*. E, *P. superbiens*. F, *P. acmodontum*. G, *P. javanicum*. H, *P. urbanianum*. I, *P. virens*. x 0.4.

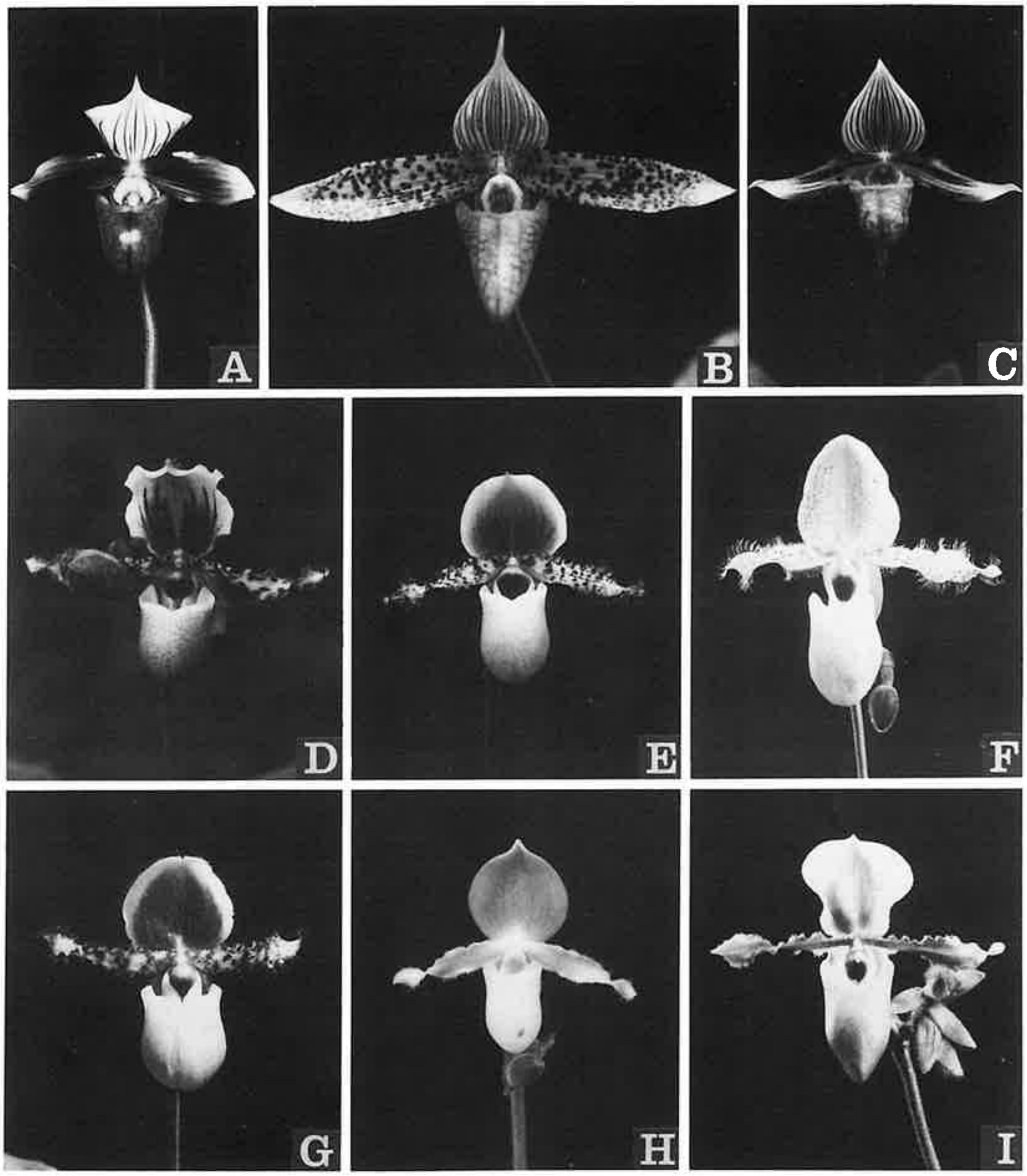

Fig. 36. Flowers of *Paphiopedilum*.
A, *P. purpuratum*. B, *P. sukhakulii*. C, *P. venustum*. D, *P. chamberlainianum*. E, *P. glaucophyllum*. F, *P.* var. *moquettianum*. G, *P. liemianum*. H, *P.* var. *primulinum*. I, *P. victoria-regina*. × 0.4.

Paphiopedilum 属4種の核形態学的研究*

唐澤耕司**

Karyomorphological studies on four species of *Paphiopedilum*

Kohji Karasawa

Paphiopedilum 属の詳細な核形態学的研究は Karasawa（1978，1979），Karasawa & Aoyama（1980）により56種5亜種1変種1品種について報告されている。

今回，新たに未報告な4種について，核形態学的観察を行ったので報告する。

材料および方法

本研究に用いた材料は表1に示す通りである。貴重な材料を提供された吉占和氏，一乗茂明氏，木村智氏と増井清氏に厚くお礼申し上げる。

研究方法は Karasawa（1979）に準じて行った。

観察結果

今回観察した4種の間期核はいずれも染色中央粒型を示し（図1B，2B，3B），前期染色体はオルセインで一様に濃染され（図1C，2C，3C，4B），本属の他の種（Karasawa 1979）と異なるところはなかった。

1．*Paphiopedilum micranthum* Tang et Wang，$2n=26$，図1，表2．

本種は中国の雲南に産し，1951年に記載されている。植物体は *P. delenatii* Guillaumin に類似する。花は白色，上萼片と側花弁には紫色の脈が入り，唇弁は特に大きくて目立つ。（図1A）。

本種の染色体数については $2n=26$ を算定した（図1D）。分裂期中期染色体について長さを測定し，その結果を表2に示した。

$2n=26$ 個の中期染色体は，長さが 12.1～3.9 μm の範囲にあり，4個の大型染色体と漸変的に小さくなっている22個の小型染色体とから構成されていた（図1E）。

第1から第4番目までの4個の大型染色体は長さが 12.1～11.3 μm までの範囲にあり，動原体はいずれも中部に位置していた。

第5から第26番目までの22個の染色体は長さが 6.8～3.9 μm までの範囲にあり，動原体はいずれも中部に位置していた。

第3，4，9，10，15，16番目の6個の染色体では長腕の基部近くに，第11，12，19，20番目の4個の染色体では短腕中部に小狭窄が観察された。また，本種では付随体は観察されなかった。

以上のように，本種の $2n=26$ 個の中期染色体は4個の大型染色体と22個の漸変的に小さくなっている小型染色体とからなる2様相核型を示している点で，本属の他の $2n=26$ の種と共通した特徴を示す。近縁の *P. delenatii* の核型に比べて，本種の $2n=26$ 個の染色体は動原体がいずれも中部に位置していることで明らかに異なっている。

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* Contribution from the Hiroshima Botanical Garden No.20

** The Hiroshima Botanical Garden

Bulletin of The Hiroshima Botanical Garden, No.5 : 70-79, 1982

Table 1. Sources, numbers of clone and chromosome number of species of *Paphiopedilum* studied.

Species	Locality	Source	No. of clone	Chromosome number (2n)
P. micranthum	Yunnan	Tsi Zhan-huo	1	26
P. armeniacum	Yunnan	Tsi Zhan-huo	1	26
		Satoshi Kimura	1	26
P. dianthum	Yunnan	Kiyoshi Masui	1	26
P. urbanianum	Philippine	Shigeaki Ichijo	1	40
		Hiroshima Bot. Gard.	1	40

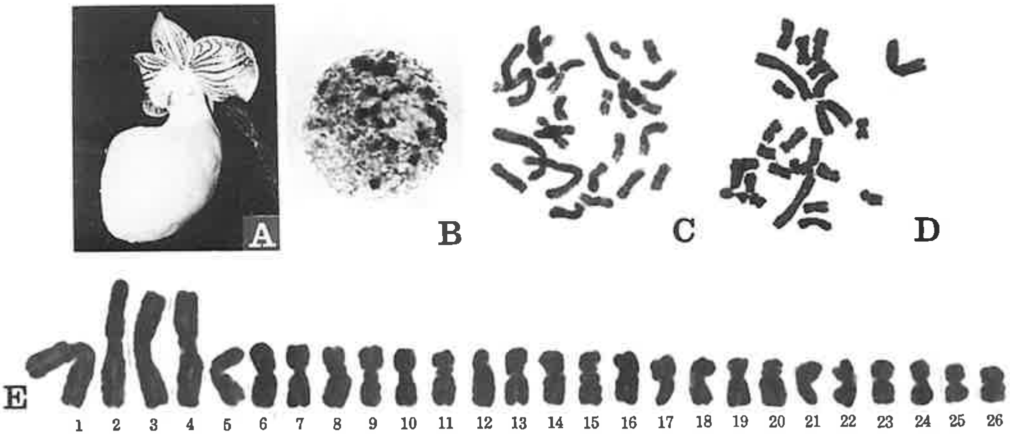

Fig. 1. Photomicrographs of the somatic chromosomes of *Paphiopedilum micranthum*. A, flower. B, chromosomes at resting stage. C, chromosomes at mitotic prophase. D, chromosomes at mitotic metaphase, 2n=26. E, individual chromosomes at mitotic metaphase.
A, x0.3. B–D, x720. E, x1200.

2．*Paphiopedilum armeniacum* Chen et Liu, 2n=26，図2，表3．

本種は1979年に中国の雲南でF. Y. Liuらによって発見され，1982年に記載された。植物体は前記*P. micranthum*に似るが，葉はより狭長で紫色がやや淡い。花は*P. delenatii*に類似し，花色が杏黄色である（図2A）。

本種の染色体数についてはChen et Liu（1982）が2n=26と報告しているが，核形態の詳細な報告はない。筆者も2個体において2n=26を算定した（図2D）。分裂期中期染色体について長さを測定し，その結果を表3に示した。

本種の2n=26個の中期染色体は長さが11.5〜4.0 μmまでの範囲にあり，4個の大型染色体と漸変的に小さくなっている22個の小型染色体とから構成されていた（図2E）。

第1から第4番目までの4個の染色体は長さが11.5〜11.1 μmまでの範囲にあり，動原体が中部に位置していた。

第5から第26番目までの22個の染色体は長さが7.9〜4.0 μmまでの範囲にあり，第5〜8，11〜16，

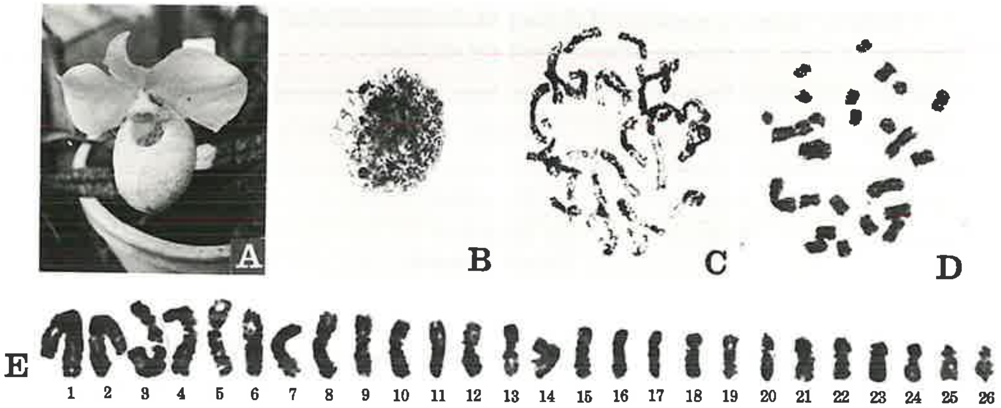

Fig. 2. Photomicrographs of the somatic chromosomes of *Paphiopedilum armeniacum*. A, flower. B, chromosomes at resting stage. C, chromosomes at mitotic prophase. D, chromosomes at mitotic metaphase, 2n=26. E, individual chromosomes at mitotic metaphase.
A, x0.3. B–D, x720. E, x1200.

21，22，25，26番目の14個の染色体は動原体が中部に位置し，第9，10，17～20，23，24番目の8個の染色体は動原体が次中部に位置していた。また，付随体染色体は観察されなかった。

以上のように，本種の2n＝26個の染色体は，前記 *P. micranthum* のそれに比べて，次中部動原体型染色体（№9，10，17－20，23，24）を8個有する点で明らかに区別される。

3．*Paphiopedilum dianthum* Tang et Wang, 2n＝26，図3，表4．

本種は中国の雲南に産し，*P. parishii* (Rchb. f.) Stein に極めて類似する。花は一般に *P. parishii* に比べて褐色味が少なく，側花弁に入る紫黒色の斑点も少数で，全体に光沢が強い（図3 A）。

本種の染色体数は2n＝26を算定した（図3 D）。分裂期中期染色体について長さを測定し，表4に示した。

2n＝26個の中期染色体は長さが14.4～5.1 μm までの範囲にあり，4個の大型染色体と漸変的に小さくなっている22個の小型染色体とから構成されていた（図3 E）。

第1から第4番目までの4個の染色体は長さが14.4～11.3 μm の範囲にあり，動原体が中部に位置していた。

第5から第26番目までの22個の染色体は長さが10.4～5.1 μm までの範囲にあり，第5～8，15～18，23～26番目の12個の染色体は動原体が中部に，第9，10，13，14，19～22番目の8個の染色体は動原体が次中部に位置し，第11，12番目の2個の染色体は動原体が次端部に位置していた。また，付随体染色体は観察されなかった。

以上のように，本種の2n＝26個の染色体は次中部動原体型染色体を8個と次端部動原体型染色体2個を含み，外部形態の類似する *P. parishii*（2n＝26，次中部動原体型染色体を6個有する）の核型と明らかに異なり，更に腕比の高い染色体から構成されている。また，本属の2n＝26個の染色体を有する種のうち，次端部動原体型染色体は本種で初めて観察されたものである。

4．*Paphiopedilum urbanianum* Fowl., 2n＝26，図4，表5．

本種は1980年に J. T. Urban によって Mindoro

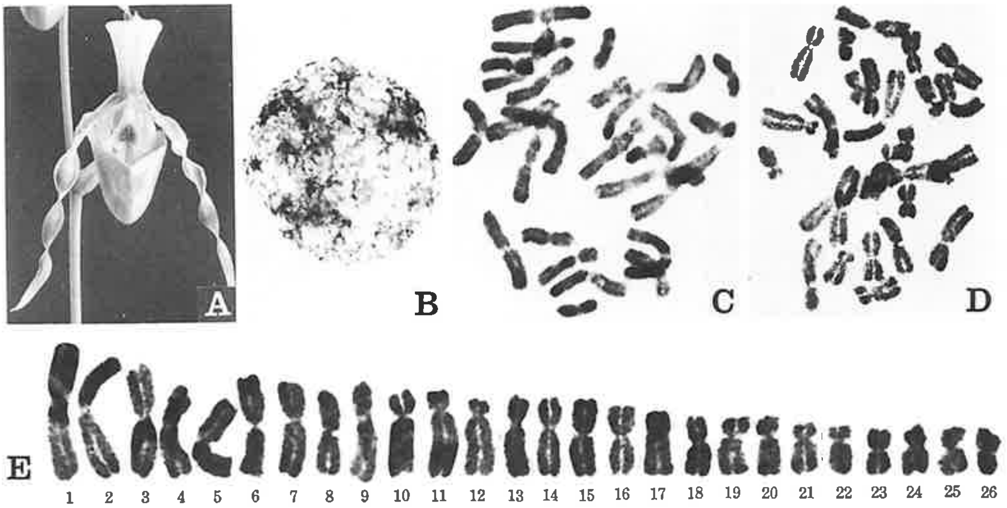

Fig. 3. Photomicrographs of the somatic chromosomes of *Paphiopedilum dianthum*. A, flower. B, chromosomes at resting stage. C, chromosomes at mitotic prophase. D, chromosomes at mitotic metaphase, 2n=26. E, individual chromosomes at mitotic metaphase.
A, ×0.3. B–D, ×720. E, ×1200.

島で発見され，1981 年に記載された。

本種の葉は狭長楕円形，その表面は濃緑色と緑白色の斑紋様となる。花は1花茎に1花つき，花径10〜12 cm。上萼片は広卵形，白色地に緑色の縦の筋が入り，側花弁は線状楕円形で斜下方に伸び，緑色で弁端は桃紫色を帯び，基部から中部にかけて濃緑色の脈と紫黒色の細点が入る。唇弁の袋の縁は外を向き，開口部の両側は耳状突出する（図4 A）。

本種の染色体数は 2n＝40 を算定した（図4 C）。分裂期中期染色体について長さを測定し，表5に示した。

第1，2番目の2個の染色体は長さがともに9.0 *μm* あり，動原体は次中部に位置していた。

第3，4番目の2個の染色体は長さが8.5 *μm* と8.3 *μm* あり，動原体は中部に位置していた。

第5〜8番目までの4個の染色体は長さが7.8〜7.3 *μm* までの範囲にあり，動原体が次中部に位置していた。

第9，10番目の2個の染色体は長さがともに7.3 *μm* あり，動原体は中部に位置していた。

第11，12番目の2個の染色体は長さがともに7.0 *μm* あり，動原体は次中部に位置していた。

第13〜40番目までの28個の染色体は長さが7.4〜4.0 *μm* までの範囲にあって漸次小さくなっており，動原体はいずれも端部に位置していた（図4 D）。

以上のように，本種の 2n＝40 個の染色体は12個の中部動原体的染色体と20個の端部動原体的染色体とからなり，2n＝40＝12V＋28I＝26V の系列に属する。近縁の *P. virens* (Rchb. f.) Pfitz. (2n＝40＝12V＋28I) のそれに比べて，6個の次中部動原体型染色体を含むことで明らかに区別される。

要　　約

1. *Paphiopedilum* 4種の核形態学的研究を行い，*P. armeniacum* で 2n＝26 を再確認し，染色体数の未報告であった3種について，*P. micranthum* 2n＝26, *P. dianthum* 2n＝26, *P. urbanianum* 2n＝40 を算定した。

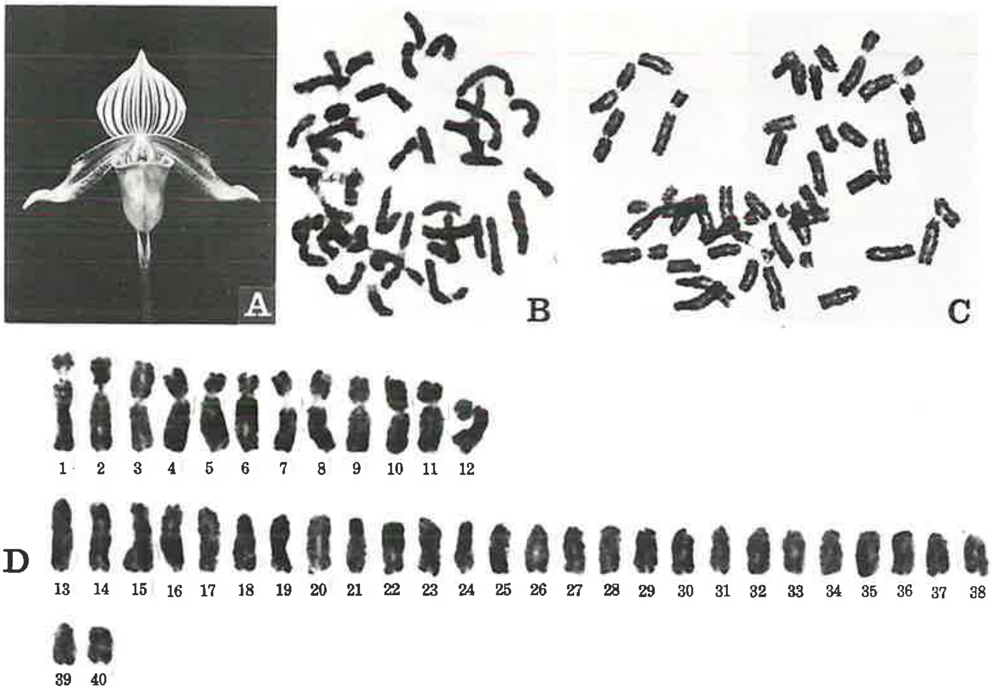

Fig. 4. Photomicrographs of the somatic chromosomes of *Paphiopedilum urbanianum*. A, flower. B, chromosomes at mitotic prophase. C, chromosomes at mitotic metaphase, 2n=40. D, individual chromosomes at mitotic metaphase. A, x0.3. B–C, x720. D, x1200.

２．*P. micranthum* の 2n＝26 個の染色体は動原体がいずれも中部に位置していたが，*P. armeniacum* 2n＝26 では次中部動原体型染色体を 8 個（No.9，10，17〜20，23，24）含み，近縁の *P. micranthum* のそれに比べて大きく構成変化がみられた。

３．*P. dianthum* の 2n＝26 個の染色体は次中部動原体型染色体を 8 個（No.9，10，13，14，19〜22）と次端部動原体型染色体を 2 個（No.11，12）含み，近縁の *P. parishii* 2n＝26 のそれに比べて，さらに腕比の高い染色体構成がみられた。また，本属の 2n＝26 の種では次端部動原体型染色体は本種で初めて観察された。

４．*P. urbanianum* の 2n＝40 個の染色体は 12V＋28I の構成からなり，12 個の V 字型染色体は 8 個（No.1，2，5〜8，11，12）の次中部動原体型染色体を含み，近縁の *P. virens* 2n＝40 に比べて，腕比の高い染色体からなり明らかに異なる核型を示していた。

Summary

1. The chromosome numbers of three species, *P. micranthum* 2n=26, *P. dianthum* 2n=26, and *P. urbanianum* 2n=40, were recorded for the first time, and *P. armeniacum* 2n=26 was redocumented.
2. The chromosome complement of the karyotype of *P. micranthum* was found to be composed of metacentric chromosomes. In contrast, that of *P. armeniacum* was composed of 18 metacentric chromosomes and 8 submetacentric chromosomes (No. 9,

10, 17〜20, 23 and 24).

3. The chromosome complement of the karyotype of *P. dianthum* (2n=26) was found to be composed of 16 metacentric chromosomes, 8 submetacentric chromosomes and two subtelocentric chromosomes. Thus, the karyotype of this species was clearly different from *P. parishii,* allied species in the same genus. The present paper is the first report of the subtelocentric chromosome in the 2n=26 species of this genus.
4. The chromosome complement of the karyotype of *P. urbanianum* (2n=40) was found to be composed of 4 metacentric chromosomes, 8 submetacentric chromosomes and 28 telocentric chromosomes. Thus, the karyotype of this species was clearly different from *P. virens* which had the same number of chromosome.

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Table 2. Measurements of somatic chromosomes of *Paphiopedilum micranthum* at metaphase, 2n=26

Chromosome	Length (μm)	Relative length	Arm ratio	Form
1	5.8 + 6.3 = 12.1	7.3	1.1	m
2	5.7 + 6.3 = 12.0	7.3	1.1	m
3	5.4 + 5.9 = 11.3	6.8	1.1	m
4	5.4 + 5.9 = 11.3	6.8	1.1	m
5	3.2 + 3.6 = 6.8	4.1	1.1	m
6	3.1 + 3.6 = 6.7	4.1	1.2	m
7	3.0 + 3.6 = 6.6	4.0	1.2	m
8	3.0 + 3.6 = 6.6	4.0	1.2	m
9	2.4 + 3.6 = 6.0	3.6	1.5	m
10	2.4 + 3.6 = 6.0	3.6	1.5	m
11	2.5 + 3.2 = 5.7	3.5	1.3	m
12	2.5 + 3.2 = 5.7	3.5	1.3	m
13	2.6 + 3.0 = 5.6	3.4	1.2	m
14	2.6 + 3.0 = 5.6	3.4	1.2	m
15	2.3 + 3.2 = 5.5	3.3	1.4	m
16	2.3 + 3.2 = 5.5	3.3	1.4	m
17	2.3 + 2.9 = 5.2	3.1	1.3	m
18	2.3 + 2.9 = 5.2	3.1	1.3	m
19	2.2 + 2.7 = 4.9	3.0	1.2	m
20	2.2 + 2.7 = 4.9	3.0	1.2	m
21	2.3 + 2.3 = 4.6	2.8	1.0	m
22	2.3 + 2.3 = 4.6	2.8	1.0	m
23	2.2 + 2.3 = 4.5	2.7	1.0	m
24	2.2 + 2.3 = 4.5	2.7	1.0	m
25	1.9 + 2.0 = 3.9	2.4	1.1	m
26	1.9 + 2.0 = 3.9	2.4	1.1	m

Table 3. Measurements of somatic chromosomes of *Paphiopedilum armeniacum* at metaphase, 2n=26

Chromosome	Length (μm)	Relative length	Arm ratio	Form
1	5.0 + 6.5 = 11.5	6.6	1.3	m
2	5.0 + 6.5 = 11.5	6.6	1.3	m
3	4.7 + 5.4 = 11.1	6.4	1.1	m
4	4.7 + 5.4 = 11.1	6.4	1.1	m
5	3.5 + 4.4 = 7.9	4.6	1.3	m
6	3.5 + 4.4 = 7.9	4.6	1.3	m
7	3.0 + 4.5 = 7.5	4.3	1.5	m
8	3.0 + 4.5 = 7.5	4.3	1.5	m
9	2.2 + 4.5 = 6.7	3.9	2.0	sm
10	2.2 + 2.4 = 6.7	3.9	2.0	sm
11	2.8 + 3.5 = 6.3	3.6	1.3	m
12	2.8 + 3.5 = 6.5	3.6	1.3	m
13	2.8 + 3.5 = 6.5	3.6	1.3	m
14	2.8 + 3.5 = 6.5	3.6	1.3	m
15	2.5 + 3.5 = 6.0	3.5	1.4	m
16	2.5 + 3.5 = 6.0	3.5	1.4	m
17	1.6 + 3.5 = 5.1	2.9	2.2	sm
18	1.6 + 3.5 = 5.1	2.9	2.2	sm
19	1.6 + 3.3 = 4.9	2.8	2.1	sm
20	1.6 + 3.3 = 4.9	2.8	2.1	sm
21	2.0 + 2.9 = 4.9	2.8	1.5	m
22	2.0 + 2.9 = 4.9	2.8	1.5	m
23	1.5 + 2.8 = 4.3	2.5	1.9	sm
24	1.5 + 2.8 = 4.3	2.5	1.9	sm
25	1.5 + 2.5 = 4.0	2.3	1.7	m
26	1.5 + 2.5 = 4.0	2.3	1.7	m

Table 4. Measurements of somatic chromosomes of *Paphiopedilum dianthum* at metaphase, 2n=26

Chromosome	Length (μm)	Relative length	Arm ratio	Form
1	6.6 + 7.8 = 14.4	6.6	1.2	m
2	6.5 + 7.6 = 14.1	6.4	1.2	m
3	5.5 + 6.4 = 11.9	5.4	1.2	m
4	5.1 + 6.2 = 11.3	5.2	1.2	m
5	5.2 + 5.2 = 10.4	4.7	1.0	m
6	5.2 + 5.2 = 10.4	4.7	1.0	m
7	4.1 + 5.5 = 9.6	4.4	1.3	m
8	4.1 + 5.2 = 9.3	4.2	1.3	m
9	3.1 + 6.4 = 9.5	4.3	2.1	sm
10	3.0 + 6.3 = 9.3	4.2	2.1	sm
11	2.0 + 7.0 = 9.0	4.1	3.5	st
12	1.9 + 6.9 = 8.8	4.0	3.6	st
13	3.1 + 5.5 = 8.6	3.9	1.8	sm
14	3.1 + 5.5 = 8.6	3.9	1.8	sm
15	3.9 + 4.5 = 8.4	3.8	1.2	m
16	3.6 + 4.4 = 8.0	3.6	1.2	m
17	3.1 + 4.0 = 7.1	3.2	1.3	m
18	3.0 + 3.9 = 6.9	3.1	1.3	m
19	2.0 + 3.9 = 5.9	2.7	2.0	sm
20	2.0 + 3.9 = 5.9	2.7	2.0	sm
21	1.8 + 3.8 = 5.6	2.6	2.1	sm
22	1.8 + 3.8 = 5.6	2.6	2.1	sm
23	2.4 + 2.9 = 5.3	2.4	1.2	m
24	2.4 + 2.9 = 5.3	2.4	1.2	m
25	2.4 + 2.7 = 5.1	2.3	1.1	m
26	2.4 + 2.7 = 5.1	2.3	1.1	m

Table 5. Measurements of somatic chromosomes of *Paphiopedilum urbanianum* at metaphase, 2n=40

Chromosome	Length (μm)	Relative length	Arm ratio	Form
1	2.5 + 6.5 = 9.0	3.8	2.6	sm
2	2.6 + 6.4 = 9.0	3.8	2.5	sm
3	3.5 + 5.0 = 8.5	3.6	1.4	m
4	3.5 + 5.0 = 8.5	3.6	1.4	m
5	2.3 + 5.5 = 7.8	3.3	2.4	sm
6	2.3 + 5.5 = 7.8	3.3	2.4	sm
7	2.5 + 4.8 = 7.3	3.1	1.9	sm
8	2.5 + 4.8 = 7.3	3.1	1.9	sm
9	2.8 + 4.5 = 7.3	3.1	1.6	m
10	3.0 + 4.3 = 7.3	3.1	1.4	m
11	2.3 + 4.7 = 7.0	2.9	2.0	sm
12	2.3 + 4.7 = 7.0	2.9	2.0	sm
13	d + 7.4 = 7.4	3.1	$<\infty$	t
14	d + 7.2 = 7.2	3.0	$<\infty$	t
15	d + 7.1 = 7.1	3.0	$<\infty$	t
16	d + 6.8 = 6.8	2.9	$<\infty$	t
17	d + 6.3 = 6.3	2.6	$<\infty$	t
18	d + 5.9 = 5.9	2.5	$<\infty$	t
19	d + 5.9 = 5.9	2.5	$<\infty$	t
20	d + 5.9 = 5.9	2.5	$<\infty$	t
21	d + 5.5 = 5.5	2.3	$<\infty$	t
22	d + 5.1 = 5.1	2.1	$<\infty$	t
23	d + 5.1 = 5.1	2.1	$<\infty$	t
24	d + 5.0 = 5.0	2.1	$<\infty$	t
25	d + 5.0 = 5.0	2.1	$<\infty$	t
26	d + 5.0 = 5.0	2.1	$<\infty$	t
27	d + 4.7 = 4.7	2.0	$<\infty$	t
28	d + 4.7 = 4.7	2.0	$<\infty$	t
29	d + 4.5 = 4.5	1.9	$<\infty$	t
30	d + 4.5 = 4.5	1.9	$<\infty$	t
31	d + 4.5 = 4.5	1.9	$<\infty$	t
32	d + 4.5 = 4.5	1.9	$<\infty$	t
33	d + 4.4 = 4.4	1.8	$<\infty$	t
34	d + 4.4 = 4.4	1.8	$<\infty$	t
35	d + 4.4 = 4.4	1.8	$<\infty$	t
36	d + 4.4 = 4.4	1.8	$<\infty$	t
37	d + 4.3 = 4.3	1.8	$<\infty$	t
38	d + 4.2 = 4.2	1.8	$<\infty$	t
39	d + 4.2 = 4.2	1.8	$<\infty$	t
40	d + 4.0 = 4.0	1.8	$<\infty$	t

d: dot

Chromosome count in *Dendrobium* II. 30 species*

Kiyoshi Hashimoto**

デンドロビウム属の染色体数 II. 30種

橋 本 清 美

In Series I of the present paper (Hashimoto 1981), the chromosome numbers of 87 species of the genus *Dendrobium* were studied. The chromosome numbers of 36 species of them were recorded for the first time and those of 14 species were redocumented. The present paper, continued from the previous paper, was undertaken to expand the chromosome number determinations of 30 species in the genus *Dendrobium.*

Acknowledgement

This work has been carried out under the direction of Professor Dr. Ryuso Tanaka of Hiroshima University, to whom the author wishes to express his sincerest gratitude. I also wish to thank Dr. Kohji Karasawa of Director of the Hiroshima Botanical Garden, to whom the author is indebted for the identification of the materials studied.

Materials and Methods

All materials identified by the observation of flowers were grown in the Hiroshima Botanical Garden. The taxonomy of the materials was followed to Schlechter (1912, 1927).

The methods for the observation of the somatic chromosomes were the same as those described in Series I.

Results and Discussion

The somatic chromosomes observed in the present investigation were shown in Fig. 1–4. Results of the chromosome counts of the species of the genus *Dendrobium* investigated were listed in alphabetical orders in Table 1. In Table 1 the previous counts appeared in papers were

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* Contribution from the Hiroshima Botanical Garden No.

** The Hiroshima Botanical Garden

Bulletin of The Hiroshima Botanical Garden, No. 5: 00 – 00, 1982

Table 1. Chromosome numbers of the species of *Dendrobium* studied.

Species	Chromosome number				Reference
	Present count		Previous count		
	2n	n	2n	n	
acinaciforme Roxb.	38			19	Mehra & Sehgal 1975
aduncum Wall. et Ldl.	38				
aggregatum Roxb.					
var. *jenkinsii* (Wall.) Ldl.	38		38		Jones 1963
baileyi F. Muell.	38				
bambusaefolium Par. et Rchb. f.	38				
bellatulum Rolfe	38				
bicameratum Ldl.	38		38		Jones 1963
					Mehra & Kashyap 1978
			40		Arora 1968
				19	Vij, Gupta & Garg 1976
bracteosum Rchb. f.	38				
capituliflorum Rolfe	38		38		Jones 1963
chameleon Ames.	38		38		Pancho 1965
coelogyne Rchb. f.	40				
cumulatum Ldl.	40				
densiflorum Wall.	40		40+2f		Kosaki 1958
	40+3f			20+(1–2f)	Mehra & Vij 1970
			38		Sharma 1970
			42		Chatterji 1976
				20	Mehra & Sehgal 1976
			40+1f		Hashimoto 1981
dixanthum Rchb. f.	40		40		Kamemoto & Sagarik 1967
	40+4f				Wilfret & Kamemoto 1971
			41		Jones 1963
			40+2f		Hashimoto 1981
gibsonii Paxt.	40		38		Vajrab. & Randolph 1960
					Sharma 1970
gouldii Rchb. f.	38		38		Kosaki 1958
					Kosaki & Kamemoto 1961
					Wilfret & Kamemoto 1971
gratiosissimum Rchb. f.	38		38		Jones 1963
					Wilfret & Kamemoto 1971
lawesii F. Muell.	38				
linguella Rchb. f.	38		38		Kamemoto & Sagarik 1967
					Wilfret & Kamemoto 1971
loddigesii Rolfe	38		40		Ito & Mutsuura 1957
			38		Jones 1963
					Banerji & Chaudhuri 1972

Table 1. (continued)

longicornu Ldl.	38	38		Jones 1963
			19	Mehra & Sehgal 1976
				Malla et al. 1977
monophyllum F. Muell.	38			
musciferum Schltr.	40			
nakaharaei Schltr.	40	30		Hsu 1972
papilio Loher	40			
phlox Schltr.	38			
rigidum Ldl.	38			
unicum Seidenf.	38			
victoriae-reginae Loher	38	38		Jones 1963
				Wilfret & Kamemoto 1971
williamsonii Day et Rchb. f.	38	38		Kosaki & Kamemoto 1961
				Kamemoto & Sagarik 1967
		57		Vij, Gupta & Garg 1976

also listed.

Among the 30 species in the genus *Dendrobium,* 22 were 2n=38, 6 were 2n=40 and the rest were other numbers such as 2n=40 and 2n=40+3f in *D. densiflorum,* 2n=40 and 2n=40+4f in *D. dixanthum.*

The chromosome numbers of following 14 species in the genus *Dendrobium* were recorded for the first time : *D. aduncum* 2n=38, *D. baileyi* 2n=38, *D. bambusaefolium* 2n=38, *D. bellatulum* 2n=38, *D. bracteosum* 2n=38, *D. coelogyne* 2n=40, *D. cumulatum* 2n=40, *D. lawesii* 2n=38, *D. monophyllum* 2n=38, *D. musciferum* 2n=40, *D. papilio* 2n=40, *D. phlox* 2n=38, *D. rigidum* 2n=38, *D. unicum* 2n=38.

The chromosome numbers of four species were here redocumented as follows : 2n=38 to 2n=40 in *D. gibsonii,* 2n=30 to 2n=40 in *D. nakaharaei,* 2n=38, 42, 40+1f, 40+2f to 2n=40 and 2n=40+3f in *D. densiflorum,* 2n=40, 41, 40+2f to 2n=40+4f in *D. dixanthum.* The chromosome numbers of 2n=40, 2n=40+1f and 2n=40+3f in *D. densiflorum* and 2n=40, 2n=40+2f and 2n=40+4f in *D. dixanthum* might have been natural variants, since each plant investigated was collected in the native localities of Thailand.

Summary

1. Chromosome counts were carried out in 30 species of *Dendrobium.*
2. Among these 30 species in the genus *Dendrobium,* 22 were 2n=38, 6 were 2n=40, one was both 2n=40 and 2n=40+3f and the rest one was both 2n=40 and 2n=40+4f.
3. The chromosome numbers of the 14 species of the genus *Dendrobium* were recorded for the first time and those of four species were redocumented.

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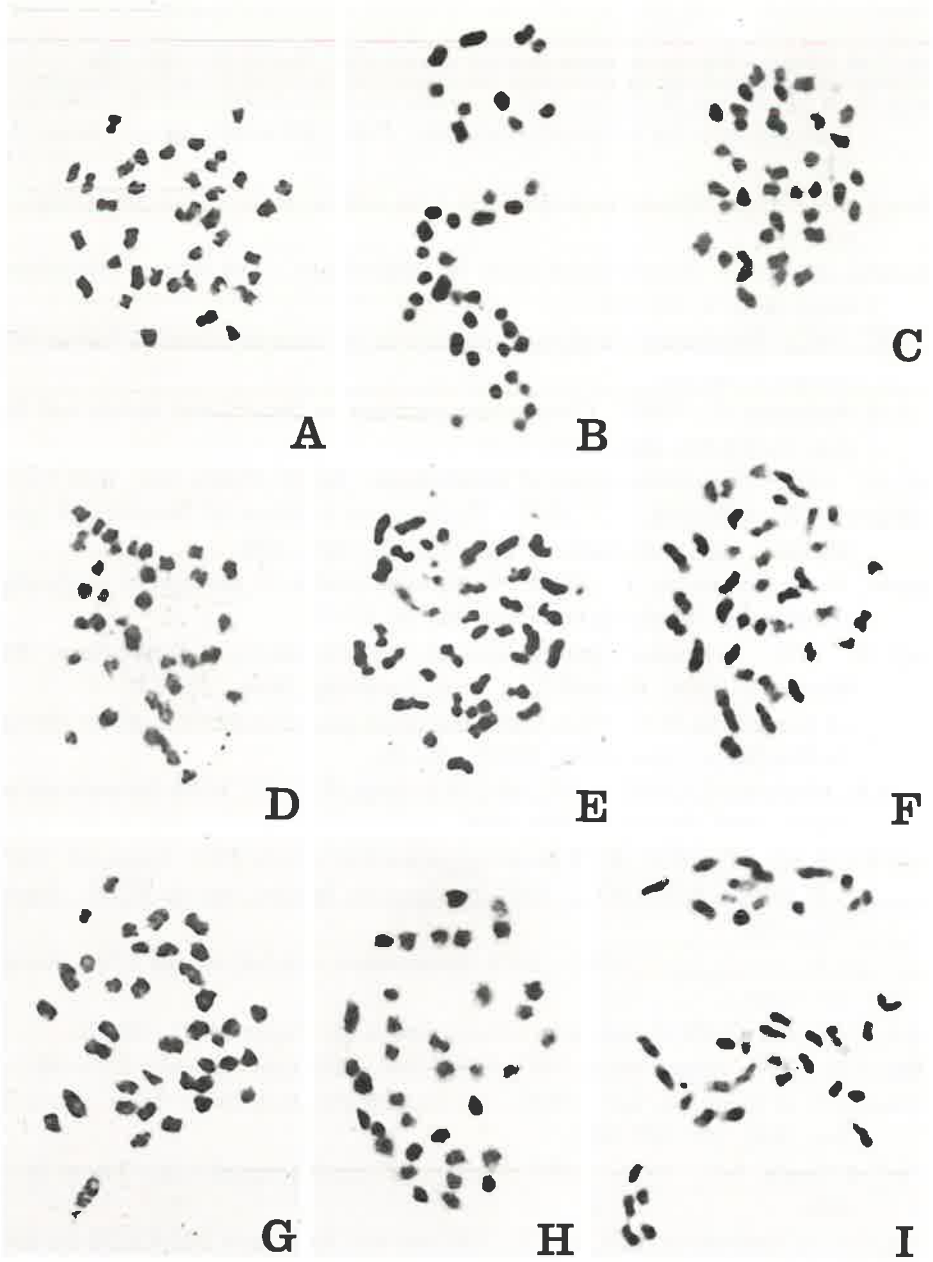

Fig. 1. Photomicrographs of somatic chromosomes of *Dendrobium*. × 2000.
A, *D. acinaciforme* 2n=38. B, *D. aduncum* 2n=38. C, *D. aggregatum* var. *jenkinsii* 2n=38. D, *D. baileyi* 2n=38. E, *D. bambusaefolium* 2n=38. F, *D. bellatulum* 2n=38. G, *D. bicameratum* 2n=38. H, *D. bracteosum* 2n=38. I, *D. capituliflorum* 2n=40.

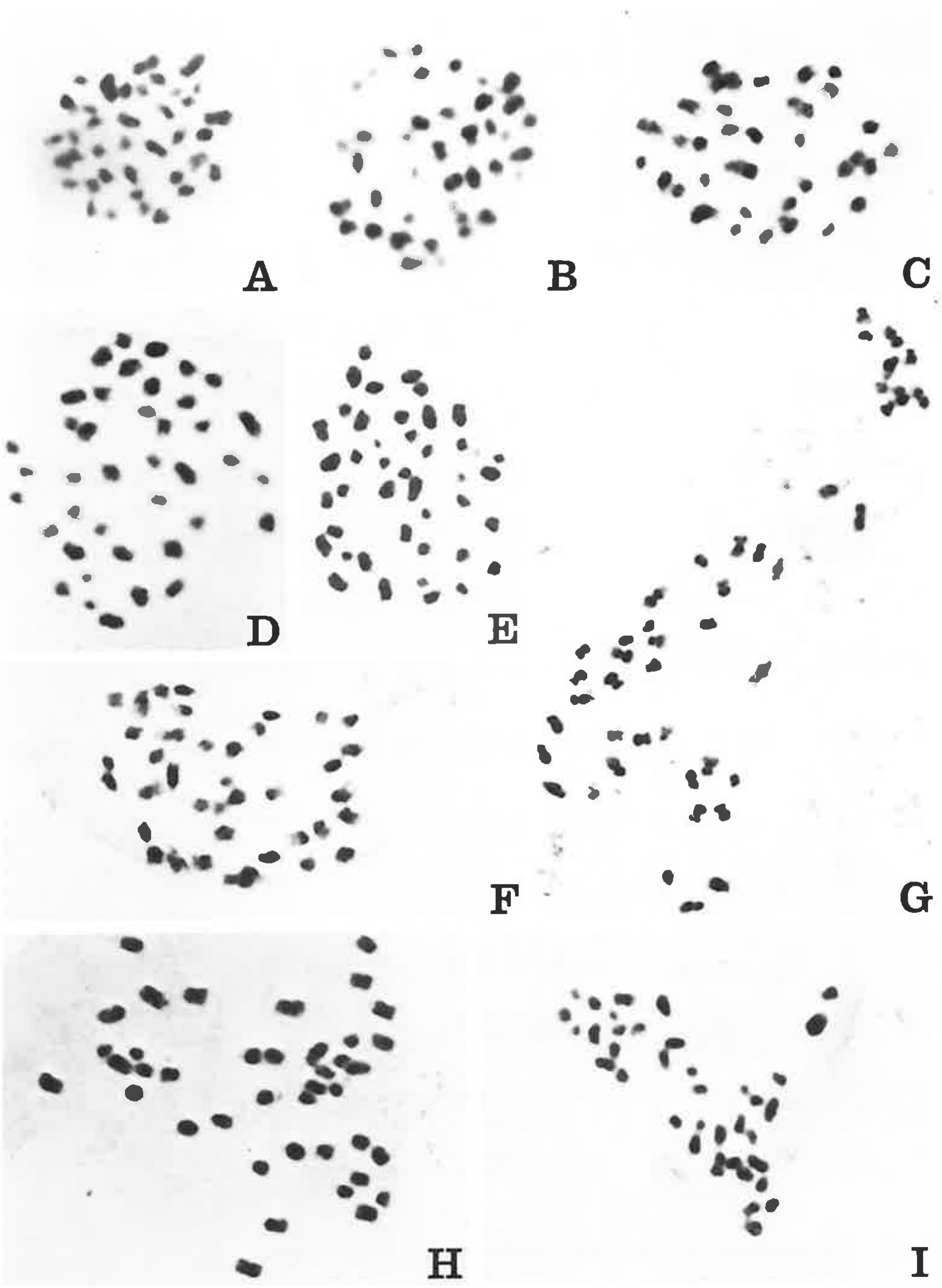

Fig. 2. Photomicrographs of somatic chromosomes of *Dendrobium*. × 2000.
A, *D. chameleon* 2n=38. B, *D. coelogyne* 2n=40. C, *D. cumulatum* 2n=40. D, *D. densiflorum* 2n=40. E, *D. densiflorum* 2n=40+3f. F, *D. dixanthum* 2n=40. G, *D. dixanthum* 2n=40+4f. H, *D. gibsonii* 2n=40. I, *D. gouldii* 2n=38.

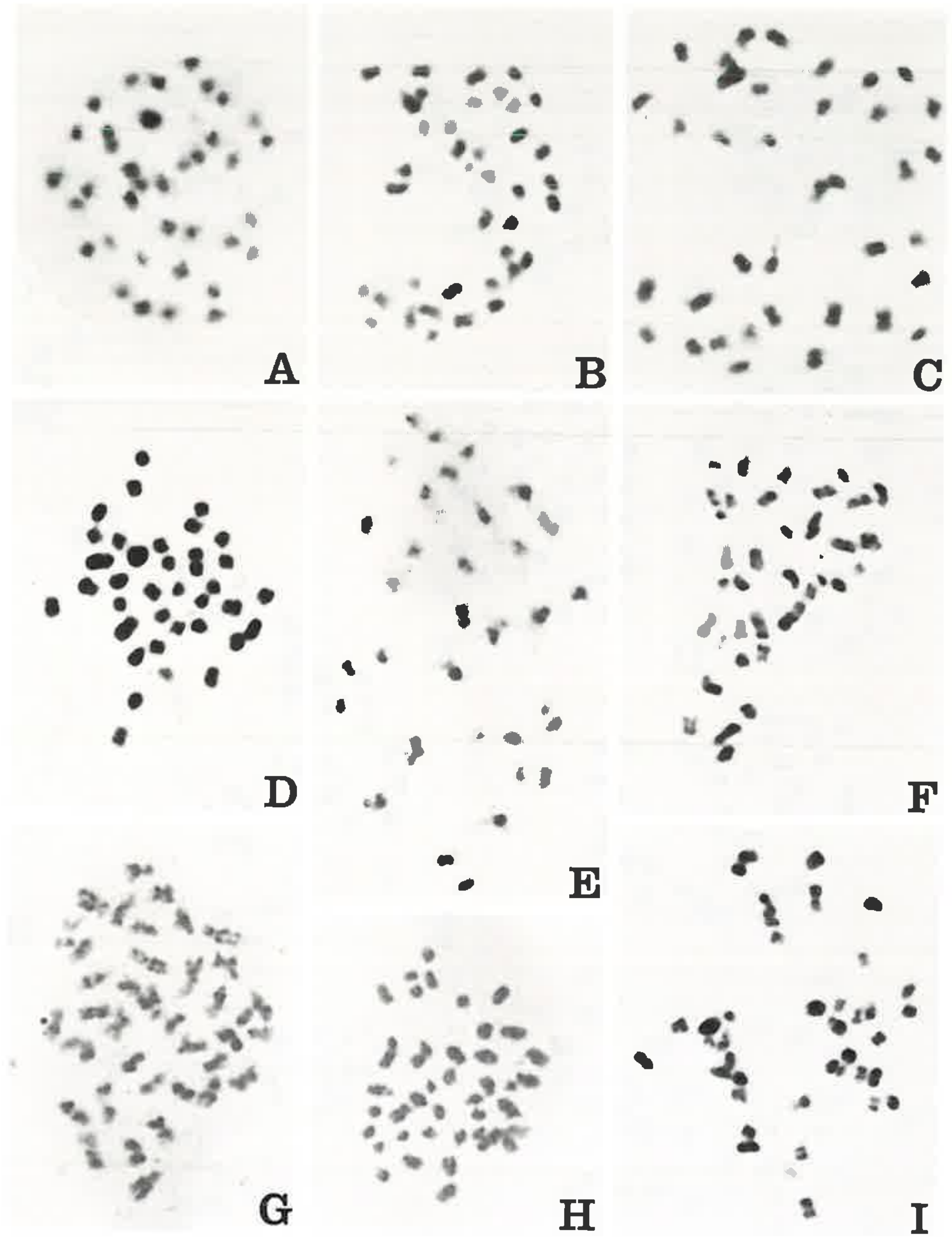

Fig. 3. Photomicrographs of somatic chromosomes of *Dendrobium*. × 2000.
A, *D. gratiosissimum* 2n=38. B, *D. lawesii* 2n=38. C, *D. linguella* 2n=38. D, *D. loddigesii* 2n=38. E, *D. longicornu* 2n=38. F, *D. monophyllum* 2n=38. G, *D. musciferum* 2n=40. H, *D. nakaharaei* 2n=40. I, *D. papilio* 2n=40.

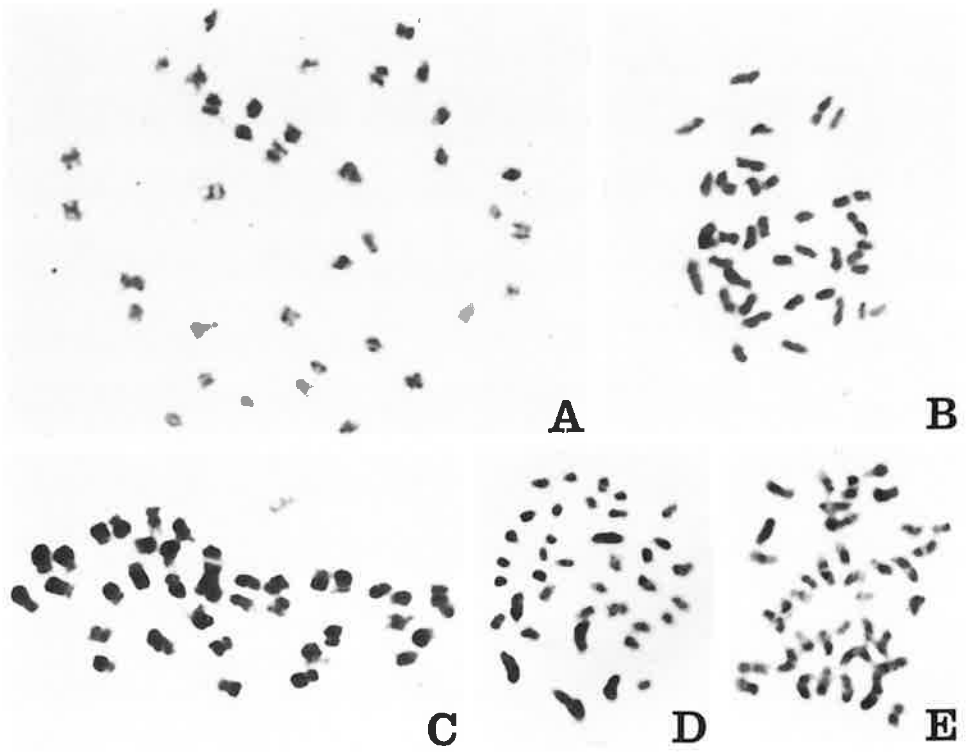

Fig. 4. Photomicrographs of somatic chromosomes of *Dendrobium*. × 2000.
A, *D. phlox* 2n=38. B, *D. rigidum* 2n=38. C, *D. unicum* 2n=38. D, *D. victoriae-reginae* 2n=38. E, *D. williamsonii* 2n=38.

広島市植物公園紀要
第5号
昭和57年12月31日　印刷発行

編集兼発行　**広島市植物公園**
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（082） 277－6954

広島市植物公園 紀要

第５号

1982

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