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GENOME AND KARYOTYPE RELATIONSHIPS

IN THE

GENUS DENDROBIUM (ORCHIDACEAE)

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By

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Genome and Karyotype Relationships in the Genus Dendrobium (Orchidaceae)

Abstract

Investigations on sexual compatability, karyotype analysis, and genome relationships were made with species in the genus Dendrobium of the family Orchidaceae.

A hybridization study was made utilizing 38 species of 10 taxonomic sections in 48 combinations. A total of 783 pollinations was made with 164 fruits harvested, of which 113 produced viable crosses. Five intrasectional and 20 intersectional combinations resulted in viable seedlings. The Eugenanthe x Eugenanthe combination showed little compatability among the species within the section and showed equal or more compatability with the Ceratobium, Phalaenanthe, and Pedilonum sections. Species in the Ceratobium section crossed as readily with species in the Phalaenanthe section as within the Ceratobium section. The percentage of non-aborted embryos was determined for each fruit harvested. The separation of all the species into the classical taxonomic sections of the genus was not possible on the basis of their crossability or percentage of non-aborted embryos.

Chromosome numbers of 33 species in 11 sections were determined, of which 31 were 2n=38 and 2 were 2n=40. Five of these had not previously been reported.

Detailed examinations of chromosome morphology were made of 23 species in 11 sections. The mean chromosome size was as variable within the sections as between the sections. The sections could not be distinguished by the average chromosome length of their constituents. No relationship was found between chromosome size and geographical and

climatological distribution in the species studied.

A mean S% and F% for each species and the average for each section was calculated. Individual sections could not be distinguished on the basis of S% and F% although a few individual species could be detected by these values in conjunction with other morphological characteristics of the karyotypes. The evolution of the karyotypes was not reflected in the external morphological specializations of the sections.

Meiosis in four intrasectional Ceratobium hybrids consistently showed 19 bivalents and the products of meiosis were normal tetrads with 19 chromosomes distributed to each microspore. Five intersectional Phalaenanthe x Ceratobium hybrids displayed an average of 16.80 bivalents and 4.40 univalents. Microspore division exhibited an average of 93.2% tetrads and 3.9% dyads, with tetrads and dyads with microcytes also observed. Meiosis in a Phalaenanthe x Latourea hybrid showed 2.06 bivalents and 33.88 univalents with the products of meiosis being tetrads, dyads, and tetrads and dyads with microcytes. Heterochromatic and heteromorphic bivalents were observed in the intersectional hybrids. The results indicated that the genomes within the Ceratobium are closely homologous; the genomes of Ceratobium and Phalaenanthe are closely related; and the genomes of Latourea are more closely related to Ceratobium than Phalaenanthe.

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INTRODUCTION

Dendrobium is one of the largest genera in the family Orchidaceae, with estimates of the number of valid species ranging from eight hundred to upwards of sixteen hundred. The genus is widely distributed from Japan in the north to Tasmania in the south, and from the foothills of the Himalayas in the west to many of the island groups of Polynesia in the east. It is an Old World genus. The habitats of the genus range from hot sea-level areas to cool mountain heights, and, as would be expected with such a varied ecological distribution, it exhibits diverse vegetative and floral structures.

The genus is characterized by being epiphytic with stems sometimes short and pseudobulbous or elongated and jointed from the rhizome. The leaves are generally short and fleshy and may be either persistent or deciduous with growth terminated in one season. The flowers are borne either near the apex of the stem or from the top of the pseudobulb and are on terminal or lateral racemes. Flower number may be one, two, or numerous. The sepals are of almost equal length with the lateral sepals adnate to the foot of the column, forming a spur. The petals, variable in color, are either larger or smaller than the sepals. The lip is movably jointed to the base of the column and is either three-lobed or entire. The stamen consists of four pollinia which are separate, free, and unappendaged (Bailey, 1964).

The genus was first monographed by Kraenzlin in 1910 although Swartz had established the genus in the eighteenth century. The work by Kraenzlin was fragmentary and subject to much criticism but it remains the most extensive and comprehensive description of the genus to date. Schlechter (1912) revised the sectional classification of the genus as presented by earlier workers (Pfitzer, 1889; Kraenzlin, 1910) and his system, based mainly on vegetative characteristics, is generally accepted today.

Most of the cytological studies on the genus have been made within the past eleven years, although the first chromosome counts of Dendrobium were recorded by Hoffmann in 1929. Chromosome numbers of 132 species have been recorded to date, with the majority of the species having a somatic number of either 38 or 40 with the remainder having numbers of 76 or 114.

The production of successful interspecific hybrids is affected by the parental genomes, and differences in chromosome number and behavior may often serve as a barrier to species cross-compatability. The results of chromosome studies are of importance to both orchid breeders and cytogeneticists.

The present study involved crossing available Dendrobium species in order to determine their sexual compatability, to examine the meiotic behavior of species hybrids, and to clarify genome relationships. The number, size, and morphology of chromosomes of species were established through karyotype analysis, and an attempt was made to correlate the evolution of karyotypes with morphological specializations of the plants. Genome, karyotype, and species relationships were examined on the basis of the present-day sectional classification of the genus.

REVIEW OF LITERATURE

The taxonomy of the genus *Dendrobium* is one of the more complex in the orchid family, due to the large number of species and the variations in their floral and vegetative morphology. Bentham and Hooker (1883) classified the genus on the basis of its reproductive structures and placed it in the Epidendrae tribe with seven sections. Schlechter (1926) proposed a classification of the orchid family divided into subtribes which were based on both reproductive and vegetative characteristics of the plants. His classification is as follows:

Subfamily	Monandrae
Division	Acrotonae
Tribe	Kerosphaereae
Series	Acanthae
Subtribe	Dendrobieae

He supported the idea that *Dendrobium* and *Eria* are closely related, based on the number of pollinia present in both genera.

A recent classification scheme of Dressler and Dodson (1960) was:

Subfamily	Orchidoideae
Tribe	Epidendreae
Subtribe	Dendrobiinae

Their classification was based on the phylogenetic characteristics of the genera. They supported Bentham and Hooker's (1883) arrangement by placing *Dendrobium* and *Bulbophyllum* in the same subtribe and creating a new subtribe for *Eria*, suggesting that the relationship between *Dendrobium* and *Bulbophyllum* is closer than that between *Dendrobium* and *Eria*.

Kraenzlin, in his monograph of the genus in 1910, divided it into eight sections and 27 subsections. He also listed five closely related genera (Appendix D). Schlechter, reviewing the orchids of Dutch New Guinea (1912), elevated four of Kraenzlin's subsections to sections, included the five related genera as sections of Dendrobium, and added 24 sections. He described 256 species which were grouped in 41 sections. Smith (1905-1939), in his report on the orchids of Java, used similar sections in describing the genus. He recorded 68 species in 11 sections, seven of which corresponded to those of Schlechter. Schlechter's sectional classification of the genus is generally adopted today.

No sexual compatability studies have been made in Dendrobium. Little research has been performed in this field for the entire orchid family. Sanford (1964) studied sexual compatability relationships in Oncidium and related genera. He analyzed all published crosses of the genus Oncidium, including intergeneric crosses, and grouped the species on the basis of their crossability. He made similar groupings on the basis of his own hybridization data. Fifty-eight species of Oncidium were arranged in four groups and six closely related genera were also grouped according to their sexual compatability with the Oncidium species. A relationship between chromosome number of the species, as reported by Sinoto (1962), and the sexual compatability groups was found. In 1967 Sanford reported on further research in Oncidium. Sixty-seven new crosses involving Oncidium species were discussed. The species involved in these new hybrids were included in the four groups previously reported. The results of the new data agreed with his original sectioning of the genus.

Hoffmann (1929, 1930) was the first to report on the chromosome complement of the genus. He reported a somatic number of 40 for five species. Miduno (1940) reported the number for two species and Eftimiu-Heim (1941) counted three species. Most of the species were reported to have 40 chromosomes. Most of the cytological information on Dendrobium has been accumulated within the last eleven years. Ito and Mutsuura (1957) published chromosome numbers of 13 species, of which 7 were 2n=38 and 6 were 2n=40.

Since 1957, the cytology of Dendrobium has attracted the attention of numerous cytologists, including Kosaki (1958), Mutsuura and Nakahira (1958, 1959), Blumenshein (1960), Vajrabhaya and Randolph (1960), Kosaki and Kamemoto (1961), Kosaki, Tanaka, and Kamemoto (1961), Dorn and Kamemoto (1962), Tanaka (1962), Jones (1963), Chardard (1963), and Shindo and Kamemoto (1963d). The results of these studies were tabulated by Tanaka and Kamemoto (1963, 1964) with 108 species of Dendrobium listed. Pancho (1965) reported counts on 18 species, 16 of which were new to the literature. Kamemoto and Sagarik (1967) recorded the chromosome numbers of 34 Dendrobium species of Thailand belonging to Callista, Eugenanthe, Nigrohirsutae, and other sections. Chromosome numbers of eight species had not been previously reported. Chromosome counts have been recorded to date for 132 species, 110 of which are 2n=38, 20 are 2n=40, 2 are 2n=76, and one is variable.

No extensive research has been done on the size and morphology of the chromosomes of Dendrobium species. Ito and Mutsuura (1957) noticed a difference in size of chromosomes in different species. Kosaki (1958) observed that most of the species he examined had minute chromosomes, but D. macrophyllum, D. spectabile, and D. superbum (anosmum) had chromosomes that were three to four times as large as the others. Shindo and Kamemoto (1963d) observed conspicuous differences in chromosome size in root tip cells of species. The chromosomes of D. formosum were twice as large as those of D. sanderae, while those of D. draconis were of intermediate size. Kosaki (1958) postulated that the size difference of chromosomes of the species may account for the incompatability in hybridization and may serve as a basis for taxonomic classification of the species.

Various researchers have shown that it is possible to detect differences in chromosome size and morphology through detailed analysis. The early work in the genus Paphiopedilum by Duncan and MacLeod (1948a, 1948b, 1949a, 1949b, 1950a, 1950b) showed that the species of this genus differ in their chromosome morphology. They divided the North American continental species with solid green leaves into smaller sections based on certain chromosome similarities (1949a). They also reported that an increase in one-armed (terminal) chromosomes showed a decrease in two-armed (median) chromosomes, although noting that one cannot say two particular one-armed chromosomes represent an ancestral two-armed chromosome which has been broken transversely at the primary constriction (1950a).

Kamemoto, Sagarik, and Dieutrakul (1963) studied the karyotypes of eight indigenous Paphiopedilum species of Thailand and divided them into three groups, based on chromosome number and morphology. They found that an increase in chromosome number was associated with a corresponding decrease in two-armed chromosomes and an increase in one-armed chromosomes.

Shindo and Kamemoto (1963a) and Kamemoto (1963) studied the chromosome morphology of 11 species of the subtribe Sarcanthinae and found similarity of karyotypes of terete-leaved species, similarity of strap-leaved Vanda, Ascocentrum, and Neofinetia, and a wide divergence of the two groups. They were able to correlate the differences of karyotypes in the groups with specializations in external morphology, using absolute chromosome size and karyotype symmetry as the basis of their correlations.

Shindo and Kamemoto (1963e) analyzed the somatic chromosomes of nine species of Phalaenopsis, six of which were native to the Philippines. They separated the species into two groups, based on chromosome size and symmetry. The chromosomes of the extra-Philippine species were two to three times larger than those of the Philippine species and the karyotypes of the former were less symmetrical with a lower F%. Differences in karyotypes between the two species were so great that no phylogenetic relationships between species of the two groups could be deduced.

Reports on the chromosome affinity at Metaphase I and the distribution of chromosomes to the microspores have appeared on Dendrobium species and primary hybrids. Dorn and Kamemoto (1962) observed the chromosomes in meiosis and microspore division of four intersectional hybrids. They reported a range of 15.3 to 17.9 bivalents at Metaphase I in the Phalaenanthe and Ceratobium intersectional hybrids. The percentage of tetrads in microspore division was between 75.6 and 93.4.

Shindo and Kamemoto (1963d) studied meiosis of four species and four primary hybrids belonging to the section Nigrohirsutae and tried to clarify the genome relationships of these species. The four species exhibited normal bivalents in meiosis while the primary hybrids showed irregularity, with a range of $0.3_{III} + 15.9_{II} + 6.9_{I}$ to 20_{II}. They concluded that the Philippine species are more closely related to each other while the one extra-Philippine species, D. formosum, is more distantly related.

Kamemoto, Shindo, and Kosaki (1964) examined meiosis in eleven species and twenty primary hybrids of Dendrobium, representing the sections Ceratobium, Phalaenanthe, and Latourea. Meiosis in the eleven species showed consistently 19 bivalent chromosomes at Metaphase I. The products of meiosis were normal tetrads with 19 chromosomes distributed in each microspore. Meiosis of ten intrasectional diploid hybrids of Ceratobium showed regular pairing at meiosis and normal tetrads were formed. The seven intersectional hybrids involving Phalaenanthe and Ceratobium exhibited similarly irregular meiotic behavior. Bivalents, univalents, and occasionally trivalents were observed. The range of mean number of bivalents was 15.7 to 18.9 with an average of 17.8. The products of meiosis were generally tetrads with the percentage of spore tetrads ranging from 64 to 95. The intersectional hybrid between Ceratobium and Latourea varied in number of bivalents from 7 to 14 with a mean of 10.8. Dyads and a few tetrads were the common products of meiosis. Chromosome pairing of the intersectional hybrid of Phalaenanthe and Latourea was highly irregular. The number of bivalents ranged from 0 to 7 with a mean of 1.8. Microspore divisions showed mostly dyads, but monads, triads, and tetrads were also observed.

Related studies on genome relationships in the Orchidaceae have been on inter- and intrageneric hybrids within the Vanda alliance (Shindo and Kamemoto, 1962, 1963a, 1963b; Kamemoto and Shindo, 1962, 1964; Tanaka and Kamemoto, 1961; Storey, Kamemoto, and Shindo, 1963).

By studying the degree of chromosome homology through pairing at Metaphase I, genome relationships between species have been clarified.

MATERIALS AND METHODS

Plant Material

Dendrobium species and hybrids used in this research were primarily available at the University of Hawaii, where a large collection of over one hundred species is maintained. Most of the species were obtained from Thailand from 1962 to 1965. The remainder of the species were donated or loaned by orchid growers in Hawaii and other parts of the United States. Other specimens were obtained from Foster Botanical Garden of Honolulu and from private and commercial orchid establishments in Hawaii.

Included in the *Dendrobium* collection at the University were 102 species representing 14 sections as classified by Schlechter (1912). The species used in this text are listed in Table I with authors and original places of publication. In addition to the species, eight primary hybrids (first generation species hybrids) were available. Four of these hybrids were intersectional, between the Ceratobium and Phalaenanthe groups; the remaining four were within the Ceratobium section.

Chromosome counts and karyotype analyses were made from the somatic cells of actively growing root tips of the species. In the primary hybrids, microsporocyte material was examined to obtain information about the meiotic behavior of the chromosomes.

Technique

Sexual compatability studies were made by using all of the flowering species present in the University collection as well as a

Table I. Alphabetical list of Dendrobium species mentioned in this text with authors and original places of publication.

Genus and Species	Author	Place of Publication
Dendrobium	O. Swartz	Nov. Act. Soc. Sc. Upsal. 6:82. 1799.
aggregatum	W. Roxburgh	Fl. Ind. Bat. 3:477. 1832.
anosmum	J. Lindley	Bot. Reg. 21:41. 1844.
arachnites	H. Reichenbach	Gard. Chron. (pt. 2), p. 354, 1874.
bellatulum	R. Rolfe	Journ. Linn. Soc. 36:10. 1903.
biggibum	J. Lindley	Paxt. Fl. Gard. 3:25. 1852.
bullenianum	H. Reichenbach	Bot. Ztg. 20:214. 1862.
canaliculatum	R. Brown	Prodr. Fl. Nov. Holl., p. 333, 1810.
cariniferum	H. Reichenbach	Gard. Chron., p. 611, 1869.
chrysotoxum	J. Lindley	Bot. Reg., t. 36, 1847.
crumenatum	O. Swartz	Schrad. Journ. Bot. 2:237. 1799.
d'albertsii	H. Reichenbach	Gard. Chron. (pt. 1), p. 366, 1878.
delacourii	A. Guillaumin	Bull. Mus. Paris, p. 522, 1924.
distichum	H. Reichenbach	Linnaea 41:39. 1877.
dixanthum	H. Reichenbach	Gard. Chron., p. 674, 1865.
draconis	H. Reichenbach	Bot. Ztg., p. 214, 1862.
farmeri	J. Paxton	Belg. Hort., p. 321, 1860.
fimbriatum	W. Hooker	Exot. Fl. 1, t. 71, 1823.
formosum	W. Roxburgh	Wall. Cat. No. 1998, 1828.
friedericksianum	H. Reichenbach	Gard. Chron. (pt. 2), p. 648, 1887.
gouldii	H. Reichenbach	Gard. Chron., p. 901, 1867.
heterocarpum	N. Wallich	Gen. & Sp. Orch., p. 78, 1830.
hildebrandii	R. Rolfe	Kew Bull., p. 182, 1894.
johannis	H. Reichenbach	Gard. Chron., p. 890, 1865.
johnsoniae	F. von Mueller	Wing's S. Sci. Rec. 2:95. 1882.

Table I. (Continued) Alphabetical list of Dendrobium species mentioned in this text with authors and original places of publication.

Genus and Specis	Author	Place of Publication
Dendrobium (continued)		
leonis	H. Reichenbach	Walp. Ann. 6:280. 1861.
linguella	H. Reichenbach	Gard. Chron. (pt. 2), p. 552, 1882.
lituiflorum	J. Lindley	Gard. Chron., p. 372, 1856.
macarthiae	Thwaites	Bot. Mag., t. 4886, 1855.
macrophyllum	A. Richard	Sert. Astrol., p. 22, 1834.
macrostachyum	J. Lindley	Gen. & Sp. Orch., p. 78, 1830.
mirbellianum	Gaudichaud	Freyc. voy., p. 423, 1826.
monile	F. Kraenzlin	Pflanzenreich 45:50. 1910.
moschatum	O. Swartz	Schrad. Neu. Journ. 1:94. 1806.
parishii	H. Reichenbach	Bot. Ztg. 21:277. 1863.
phalaenopsis	Fitzgerald	Gard. Chron. (pt. 2), p. 38, 1880.
primulinum	J. Lindley	Gard. Chron., p. 223, 1858.
senile	Parish and Reichenbach	Gard. Chron., p. 434, 1865.
spectabile	F. Miquel	Fl. Ind. Bat. 3:645. 1855.
stratiotes	H. Reichenbach	Gard. Chron. (pt. 1), p. 266, 1886.
strebloceras	H. Reichenbach	Gard. Chron. (pt. 1), p. 266, 1886.
sutepense	R. Rolfe	Kew Bull., p. 374, 1925.
tortile	J. Lindley	Gard. Chron., p. 797, 1847.
trigonopus	H. Reichenbach	Gard. Chron. (pt. 2), p. 682, 1887.
undulatum	R. Brown	Prodr. Fl. Nov. Holl., p. 332, 1810.
victoriae-reginae	Loher	Gard. Chron. (pt. 1), p. 399, 1897.

few pollinia provided by private orchid growers in Hawaii. When the number of flowers permitted, all possible crossing combinations and their reciprocals were made, including selfing. Since many of the species failed to flower at the same time, some of the pollinia were stored for later use. The anther caps were removed and the pollinia were placed in small (No. 00) gelatin capsules which in turn were enclosed in seed envelopes. These packages were stored in a 3x4x8 inch closed plastic container at 7° C. Two small packets of calcium chloride, approximately five grams each, were added to the container to prevent the accumulation of moisture. Pollinia used up to six months from the time of collection produced viable seeds and healthy seedlings.

The date of pollination, the date of abscission if the ovary did not develop, and the date of harvest of the fruit were recorded. All fruits were harvested three months after pollination, which is ample time for fertilization and embryo development to occur in Dendrobium (Niimoto and Sagawa, 1961). The seeds were planted in 250 ml Erlenmeyer flasks containing 100 ml of a modified Knudson C medium (Appendix E). The seedlings, grown in the mother flask until the first leaves appeared on the protocorms, were transplanted into 500 ml Erlenmeyer flasks at 60 plants per container. Three to four months later the plants were transferred to community pots and thereafter replanted when necessary.

The percentage of non-aborted embryos was determined for each fruit harvested. After most of the seed had been planted, a small amount was placed on a microscope slide in a drop of 1% aceto-orcein. A cover slip was added and enough pressure was applied to remove the air bubbles. The preparation was examined under low power (100X) and

Plate 1A. Normal and aborted seeds of Dendrobium species.

Figure:

1. Normal seed of D. phalaenopsis (150X).
2. Normal seed of D. macrophyllum (220X).
3. Aborted seed of D. phalaenopsis (150X).
4. Unfertilized ovules of D. phalaenopsis (175X).

Plate 1B. Culture of primary hybrids from seed to flowering (0.2X).

5. Culture from fruits to transflasking of seedlings.
6. Culture of seedlings in community pots.
7. Culture of seedlings from individual pots to flowering.

[redacted]

the percentage of developed and aborted embryos was determined (Figures 1-4).

Selection of the correct stage of bud development in which the meiotic divisions of the microsporocytes are occurring is less of a problem in Dendrobium than in plants which produce only a few flowers at any one time, such as Cattleya and Paphiopedilum. In Dendrobium, numerous flowers are generally produced on a long raceme and normally meiosis is occurring in one of the younger buds. In order to determine the proper stage of meiosis, the buds were measured from the base of the spur to the tip of the lateral sepals. In most of the hybrids, Metaphase I occurred when the buds were between 10 and 13 mm long. The length of the buds in the first post-meiotic mitosis, or microspore division, was more variable, with a range of 22 to 38 mm, depending upon the hybrid involved. A bud 10 to 11 mm long was sliced with a sharp scalpel along the entire length of the junction between the lateral sepals. Extreme caution was exercised so as not to slice the pollinia. The lateral sepals were separated and the ventral surface of the column was exposed, revealing the stigmatic cavity near the center and the pollinia at the apex.

For preliminary observations, a dissecting needle was used to remove a small portion of one pollinium which was then placed in a drop of aceto-orcein on a slide. After a cover slip was added, enough pressure was applied to flatten the cells and remove any excess stain. Observations were made under the high-dry objective (40X) to determine the stage of meiosis. If the cells were at Metaphase I, the pollinia were excised from the column and fixed in a modified Carnoy's solution

(1 part chloroform; 1 part 95% ethanol; and 2 parts glacial acetic acid) for ten minutes at 13° C., softened in 45% acetic acid for three minutes, and stained with 1% aceto-orcein. Before the cover slip was added, the mass of microsporocytes was teased with dissecting needles to separate the cells which adhere to one another in masses and do not stain satisfactorily unless well separated. The slides were stored in a closed container, which was saturated with 45% acetic acid, for ten minutes to intensify the stain. Upon removal from the container, pressure was applied to the cover slip to flatten the cells and remove any excess stain. The slide was then heated almost to boiling to obtain good differentiation between the chromosomes and the cytoplasm. When the slide cooled, it was sealed with Kerr sticky-wax. Observations were made under the oil immersion lens and the number of univalents and bivalents at Metaphase I and sporad formation were recorded.

Root-tip smears were prepared with a similar technique as that employed for the buds. Tips of actively dividing roots were cut approximately 2 mm long between 9:00 and 10:00 a.m. They were pretreated in 2 ml of 0.002 M hydroxyquinoline at 16° C. for four hours, after which they were transferred to a modified 1:1:2 Carnoy's solution at 16° C. Following a fifteen minute fixation period, the roots were hydrolyzed in one normal hydrochloric acid at 60° C. for two minutes to dissolve the intercellular pectin. The tissue was immediately washed in 45% acetic acid for three minutes, and, after removal of the root cap, placed on a slide in a drop of aceto-orcein. This was stored in a container which was saturated with 45% acetic acid for ten minutes. The slide was removed from the container and a cover slip was added. Pressure was gently applied to remove the excess stain, and after the slide was heated briefly, the cover slip was sealed with the sticky-wax.

Photomicrographs of the selected meiotic and mitotic stages were taken. Microscopic observations were made with a Leitz Wetzlar binocular microscope which was equipped with an Apo Oel 90:1 objective as well as an Apo 25:1 and an 12.5:1 objective. The microphotographs were taken with a mounted Zeiss Ikon camera with a magnification of 550X on Kodak High Contrast Copy film.

Karyotypes were made by enlarging the photomicrograph negatives to a magnification of 5500X by using a Leitz Valoy II enlarger. The chromosomes were traced on standard white botany paper and the position of the centromere was indicated. Each chromosome was measured as to the length of both the long and short arms, using 0.5 mm as the unit. The chromosomes were then arranged in descending order of length. The chromosome length of the karyotype was expressed as the mean with standard deviation, calculated on the basis of the mean chromosome length in each cell. The morphology of chromosomes of the karyotype was expressed as the mean F% with standard deviation. F% is the percentage of the short arm length over the total length of a chromosome. The chromosomes were classified into 3 groups according to the F% values: 0-30.0 (sub-terminal); 30.1-45.0 (sub-median); and 45.1-50.0 (median). S% is the percentage of the length of the smallest chromosome over the length of the largest chromosome within the karyotype. Comparisons were made as to average F%, size, and symmetry (S%) of the total karyotype.

In lieu of the herbarium voucher specimens, color slides (Kodachrome II) and black-and-white photographs (Kodak Pan-X) were taken of all species and hybrids involved in this research. Two Exakta cameras mounted on a 105 mm Xenar bellows were used for the photography. The slides and photographs, on file in the Horticulture department at the University of Hawaii, illustrate vegetative and inflorescence morphology as well as individual flower characteristics. The plants used are difficult to obtain from their Old World habitats and are too valuable as future research tools to be dried and pressed into herbarium specimens. The living collection will be maintained at the University of Hawaii.

RESULTS AND DISCUSSION

Sexual Compatability Studies

In the present hybridization study crosses involving 38 species in 10 sections were made in 44 combinations (Tables II-III; Figs. 8-75). A total of 783 pollinations, including sibling and reciprocal crosses, was made. From all of these pollinations 164 fruits were harvested, of which 113 resulted in young plantlets (Table IV). Of these 44 combinations, nine were intrasectional and 35 were intersectional. Five of the intrasectional combinations produced viable seedlings, although one, Stachyobium x Stachyobium, was a sibling cross of *D. delacourii*. Twenty of the intersectional combinations produced viable seedlings.

In the intrasectional combinations, Phalaenanthe x Phalaenanthe had the highest percentage of fruits produced per pollination, 100%, while Eugenanthe x Eugenanthe had the lowest of those that produced any fruits, 8.9%. The remaining four combinations formed 45 and 60% fruits. Germination of the seeds showed a similar relationship, with Phalaenanthe x Phalaenanthe exhibiting the highest percentage of viable crosses per pollination, 100%, and Eugenanthe x Eugenanthe one of the lowest, 4.5%. None of the Nigrohirsutae x Nigrohirsutae seeds germinated although under microscopic examination the embryos appeared to be well developed. Possibly the zygotes were not fully mature and capable of germinating at the time the pod was harvested or they were in a dormant state. The two remaining combinations, Ceratobium x Ceratobium and Latourea x Latourea, produced 60 and 57% viable crosses, respectively.

Of the intersectional crosses that produced fruits, Ceratobium

Table II. Hybrids attempted among species of Dendrobium with numbers of fruits harvested in parenthesis.

♀ \ ♂	aggregatum	arachnites	bellatulum	biggibum	bullenianum	cariniferum	chrysotoxum
aggregatum	3	1		1	1	1	2
arachnites	1	1			1	1	2
bullenianum		1	1	1	1	1	1
cariniferum			1				
chrysotoxum	2	1		1	1	1	10
d'albertsii	1	1		1 (1)	2	1 (1)	2
delacourii	1	1	1	1	1	1	1 (1)
dixanthum	1			1	1	1	1
draconis	1		1			2 (2)	2 (1)
farmeri	1						
fimbriatum	1						
formosum							1
friedericksianum							1
gouldii		1	1	1	1	1	1
grantii				1 (1)			1
heterocarpum							1
linguella	1	1 (1)					1
lituiflorum						1	1
macrophyllum	1	1		1 (1)			1 (1)
macrostachyum	1 (1)	1	1	1 (1)	3 (2)	1	1 (1)
monile	1	1	1	1	1	1	1
parishii	1	1		1	1		2
phalaenopsis	1 (1)	1 (1)	1	2 (2)	1	1 (1)	3
primulinum	1						
senile	1						
spectabile	2	1				1	2 (2)
stratiotes	1	1			1		2
strebloceras	3 (2)	1	1	1 (1)	2	1 (1)	3 (3)
undulatum	3	1	1		2	1	3 (3)
undulatum #2							1 (1)

Table II. (Continued) Hybrids attempted among species of Dendrobium with numbers of fruits harvested in parenthesis.

♀ \ ♂	crumenatum	d'albertsii	delacourii	dixanthum	draconis	farmeri	fimbriatum
aggregatum		1	1	1	1	1	1
arachnites		1	1	1		1	
bellatulum				1	1 (1)		
bullenianum	1	1		1 (1)	1 (1)	1	
cariniferum					1 (1)		
chrysotoxum	1	2	1	1	2	3	1
d'albertsii	1	1 (1)	3	1	1	1	1
delacourii		2	2 (1)	1	1	1	
dixanthum	1	1	1	3 (1)	1	1	1
draconis		1	1	1	3 (1)		
farmeri		1 (1)		1		1	1
fimbriatum		1	1				1
formosum		1	1				
friedericksianum				1	1		1
gouldii		1 (1)	1	1	1	1	
grantii		1	1				
heterocarpum		1	1		1		
linguella		1	1	1	1		1
macrophyllum		1 (1)	1 (1)	1 (1)	1 (1)	1	1
macrostachyum	3 (2)	1 (1)	3 (1)	1 (1)	1	1	1
monile		1	2	1	1	1	1
parishii		1	1	1	1		1
phalaenopsis	1	1 (1)	2	1 (1)	3 (2)	1 (1)	1 (1)
primulinum			1		1		1
spectabile		2 (1)	1	1 (1)	1	1	2
stratiotes		1 (1)	1		1		
strebloceras	3	2 (1)	2 (2)	1 (1)	1 (1)	1	1
undulatum	2	1 (1)	1	1 (1)		1 (1)	1
undulatum #2		1 (1)					

Table II. (Continued Hybrids attempted among species of Dendrobium with numbers of fruits harvested in parenthesis.

♀ \ ♂	formosum	friedericksianum	gouldii	grantii	heterocarpum	hildebrandii	leonis
aggregatum	1	1	1	1	1	1	
arachnites		1				1	
bullenianum	1	1				1	
cariniferum	1						
chrysotoxum		1		1	1	1	
d'albertsii	1	1		1	1		
delacourii	1	1		1		1	
dixanthum	1						
draconis	1						
farmeri	1						
fimbriatum		1					
formosum				1			
gouldii	1		1 (1)		1		
hildebrandii		1				1 (1)	
leonis							1
linguella					1	1	
lituiflorum		1					
macrophyllum	1			1	1	1	
macrostachyum	1	1		1	1	1	
monile	1			1	1	1	
parishii	1				1	1	
phalaenopsis	1	1		4 (4)	3	1	1
senile							
spectabile	1	1				1	
stratiotes							
strebloceras	2 (1)	1		1 (1)	1	1	1
undulatum	1	1			1	1 (1)	1

Table II. (Continued) Hybrids attempted among species of Dendrobium with numbers of fruits harvested in parenthesis.

♀ \ ♂	linguella	lituiflorum	macarthiae	macrophyllum	macrostachyum	monile	moschatum
aggregatum	1	1		1	2	1	1
arachnites	1	1			1	1	
bullenianum	1	1	1	1	1 (1)	1 (1)	
cariniferum							
chrysotoxum	1	1		1	2	1	
d'albertsii	3	1	1	4	3	1	1
delacourii	1	1		1	3	2	1
dixanthum	1	1		1	1	1	
draconis				1	2		1
farmeri				1	1	1	
fimbriatum				1			
formosum				1			
friedericksianum					1		
gouldii	1	1		1	1	1	1
grantii	1			1	1 (1)		
heterocarpum				1			
linguella	2	1		1	2	1	
lituiflorum		2					
macrophyllum	1	1		2 (1)	1	1	
macrostachyum	1 (1)	1	3	1	2 (1)	2 (1)	1
monile	1	1	1	1	1	2	
parishii	1	1		1	1	1	1
phalaenopsis	1 (1)	1	1	2	1 (1)	1	2
primulinum							
senile				1			
spectabile	1	1		2	1	1	
stratiotes				2	1		
strebloceras	2	1	1	4	2 (1)	1	1
undulatum	1	1	1	1	1 (1)	1	1
undulatum #2				1	1 (1)	1	

Table II. (Continued) Hybrids attempted among species of Dendrobium with numbers of fruits harvested in parenthesis.

♀ \ ♂	parishii	phalaenopsis	primulinum	senile	spectabile	stratiotes	strebloceras
aggregatum	1	1	1	1	1	1	1
arachnites	1	1			1	1	1
bullenianum	1	1			1		1 (1)
cariniferum							1
chrysotoxum	2	2	1		1	1	1
d'albertsii	3 (2)	2 (1)	1		3	1	2 (1)
delacourii	2 (1)	2 (1)	1		2	1	1 (1)
dixanthum	1	1	1		1		1
draconis		1 (1)			1		1
farmeri	1	1	1	1	1		1
fimbriatum		1			1		1
formosum	1	1 (1)					
friedericksianum					1		1 (1)
gouldii	1 (1)	2 (1)	1		1	1	1 (1)
grantii	1	1 (1)			1		1 (1)
heterocarpum							1 (1)
linguella	1	1			1	1	1
lituiflorum		1			1		
macrophyllum	1	2 (1)	1	1 (1)	1 (1)	1 (1)	1 (1)
macrostachyum	1 (1)	2	1		2	1	1 (1)
monile	1	1			1		1
parishii	3	1	1		1		1
phalaenopsis	1 (1)	9 (9)	1 (1)	1	1	1 (1)	1 (1)
primulinum		1	1		1		1
senile		1					1
spectabile	1	2	1		2 (2)	1 (1)	1 (1)
stratiotes	1 (1)	1 (1)			2	2 (1)	1 (1)
strebloceras	2 (1)	1 (1)	1	1	2 (1)	1	2 (1)
undulatum	1	1 (1)	1 (1)	1	3	1 (1)	1 (1)
undulatum #2		1 (1)			1 (1)	1 (1)	1 (1)

Table II. (Continued) Hybrids attempted among species of Dendrobium with number of fruits harvested in parenthesis.

♀ \ ♂	tortile	undulatum	undulatum #2
aggregatum	1	1	1
arachnites		1	
bullenianum		1 (1)	
chrysotoxum	1	2	1
d'albertsii	1	3 (1)	1
delacourii	1	2 (1)	1
dixanthum		1	
draconis		1	1
farmeri		1	
fimbriatum		1	
gouldii	1	1 (1)	
grantii		1 (1)	1
heterocarpum		1	
hildebrandii		1	
linguella		1	1
lituiflorum		1	
macrophyllum		1 (1)	1 (1)
macrostachyum	1	1 (1)	1
monile		1	1
parishii		1	1
phalaenopsis	1	1 (1)	2
primulinum		1	
spectabile	1	1 (1)	1 (1)
stratiotes		2 (2)	
strebloceras	1	1 (1)	1 (1)
undulatum	1	3 (3)	1 (1)
undulatum #2		1 (1)	

Table III. Percent of apparently viable embryos of primary hybrids among species of Dendrobium.

♀ \ ♂	aggregatum	arachnites	biggibum	bullenianum	cariniferum	chrysotoxum	crumenatum
d'albertsii			85 (v)		0		
delacourii						80 (v)	
draconis					0	0	
grantii			95 (v)				
linguella		30 (v)					
macrophyllum			85 (v)			0.1 (v)	
macrostachyum	0			0		85 (v)	0
phalaenopsis	0	0			.01 (v)		
spectabile						1 (v)	
strebloceras	0.1 (v)*		90 (v)		.1 (v)	0.1 (v)	
undulatum						0	
undulatum #2						.01	

*Viable crosses indicated by parenthesis.

Table III. (Continued) Percent of apparently viable embryos of primary hybrids among species of <u>Dendrobium</u>.

♀ \ ♂	d'albertsii	delacourii	dixanthum	draconis	farmeri	fimbriatum	formosum
bellatulum				0			
bullenianum			.01 (v)	.01 (v)			
cariniferum				0			
delacourii		97 (v)					
dixanthum			97				
draconis				98			
farmeri	.01 (v)						
gouldii	10						
macrophyllum	30 (v)	.01	.01 (v)	20 (v)			
macrostachyum	.01 (v)	0.1 (v)	.01				
phalaenopsis	90 (v)		.01 (v)	.01 (v)	.01 (v)	.01 (v)	
spectabile	4 (v)		.01 (v)				
stratiotes	95 (v)						
strebloceras	70 (v)	30 (v)	.1 (v)	.01 (v)			.01 (v)
undulatum	80 (v)		.1 (v)		0		
undulatum #2	75 (v)						

Table III. (Continued) Percent of apparently viable embryos of primary hybrids among species of <u>Dendrobium</u>.

♀ \ ♂	gouldii	grantii	hildebrandii	linguella	lituiflorum	macrophyllum	macrostachyum
bullenianum							0.1 (v)
gouldii	96 (v)						
grantii							0
hildebrandii			99 (v)				
macrophyllum						70 (v)	
macrostachyum				0			99 (v)
phalaenopsis		60 (v)		0			0
strebloceras		95 (v)					0
undulatum			0				.01 (v)
undulatum #2							.01

Table III. (Continued) Percent of apprently viable embryos of primary hybrids among species of <u>Dendrobium</u>.

♀ \ ♂	monile	parishii	phalaenopsis	primulinum	senile
bullenianum	0				
d'albertsii		0	95 (v)		
delacourii		97	.01		
draconis			0		
formosum			0		
grantii			95 (v)		
macrophyllum			85 (v)		0
macrostachyum	0	85 (v)			
phalaenopsis		0	85 (v)	0.1 (v)	
stratiotes		0	90 (v)		
strebloceras		0	95 (v)		
undulatum			95 (v)	0	
undulatum #2			85 (v)		

Table III. (Continued) Percent of apparently viable embryos of primary hybrids among species of Dendrobium.

♀ \ ♂	spectabile	stratiotes	strebloceras	undulatum	undulatum #2
bullenianum			4 (v)	0.1 (v)	
d'albertsii			65 (v)	85 (v)	
delacourii			10 (v)	20 (v)	
friedericksianum			0		
gouldii		60	25 (v)	98 (v)	
grantii			96 (v)	99 (v)	
heterocarpum			0		
macrophyllum	85 (v)	55 (v)	40 (v)	45 (v)	50 (v)
macrostachyum			.01 (v)	.01 (v)	
phalaenopsis		40 (v)	95 (v)	70 (v)	
spectabile	95 (v)	0.1 (v)	0.1 (v)	4 (v)	0
stratiotes		99 (v)	95 (v)	99 (v)	
strebloceras	20 (v)		97 (v)	99 (v)	99 (v)
undulatum		60 (v)	96 (v)	85 (v)	90 (v)
undulatum #2	80 (v)	70 (v)	90 (v)	95 (v)	

Table IV. Dendrobium sectional crosses attempted and results.

Sections Crossed	Crosses Attempted*	Fruits Harvested		Successful Crosses	
		Number	Percentage	Number	Percentage
Aporum x Aporum	1	0	0	0	0
Aporum x Ceratobium	2	0	0	0	0
Aporum x Phalaenanthe	1	0	0	0	0
Callista x Callista	28	0	0	0	0
Callista x Ceratobium	42	11	26.1	4	9.5
Callista x Eugenanthe	63	2	3.1	1	1.6
Callista x Latourea	14	3	21.4	2	14.3
Callista x Nigrohirsutae	11	1	9.0	0	0
Callista x Pedilonum	4	0	0	0	0
Callista x Phalaenanthe	11	2	18.1	1	9.1
Callista x Rhopalanthe	1	0	0	0	0
Callista x Stachyobium	5	1	20.0	1	20.0
Ceratobium x Ceratobium	43	26	60.5	26	60.5
Ceratobium x Eugenanthe	113	17	15.0	7	6.2
Ceratobium x Latourea	38	11	28.9	11	28.9
Ceratobium x Nigrohirsutae	23	4	17.3	3	13.0
Ceratobium x Pedilonum	11	2	18.2	2	18.2
Ceratobium x Phalaenanthe	24	19	79.1	16	66.7
Ceratobium x Rhopalanthe	6	0	0	0	0
Ceratobium x Stachyobium	18	4	22.2	4	22.2
Eugenanthe x Eugenanthe	89	8	8.9	4	4.5
Eugenanthe x Latourea	45	4	8.8	1	2.2
Eugenanthe x Nigrohirsutae	25	0	0	0	0
Eugenanthe x Pedilonum	17	5	29.4	2	11.8
Eugenanthe x Phalaenanthe	33	7	21.2	3	9.1
Eugenanthe x Rhopalanthe	4	2	50.0	0	0
Eugenanthe x Stachyobium	27	2	7.4	1	3.7

*Includes reciprocals and self-pollinations.

Table IV. (Continued) Dendrobium sectional crosses attempted and results.

Sections Crossed	Crosses Attempted	Fruits Harvested		Successful Crosses	
		Number	Percentage	Number	Percentage
Latourea x Latourea	7	4	57.1	4	57.1
Latourea x Nigrohirsutae	8	1	12.5	1	12.5
Latourea x Pedilonum	2	0	0	0	0
Latourea x Phalaenanthe	7	2	28.4	2	28.4
Latourea x Rhopalanthe	0	0	0	0	0
Latourea x Stachyobium	5	1	20.0	1	20.0
Nigrohirsutae x Nigrohirsutae	11	5	45.4	0	0
Nigrohirsutae x Pedilonum	4	1	25.0	1	25.0
Nigrohirsutae x Phalaenanthe	9	6	66.7	3	33.3
Nigrohirsutae x Rhopalanthe	0	0	0	0	0
Nigrohirsutae x Stachyobium	6	0	0	0	0
Pedilonum x Pedilonum	1	0	0	0	0
Pedilonum x Phalaenanthe	3	0	0	0	0
Pedilonum x Rhopalanthe	1	0	0	0	0
Pedilonum x Stachyobium	1	0	0	0	0
Phalaenanthe x Phalaenanthe	11	11	100.0	11	100.0
Phalaenanthe x Rhopalanthe	1	0	0	0	0
Phalaenanthe x Stachyobium	5	1	20.0	0	0
Rhopalanthe x Rhopalanthe	0	0	0	0	0
Rhopalanthe x Stachyobium	0	0	0	0	0
Stachyobium x Stachyobium	2	1	50.0	1	50.0

Plate 2. Vegetative and floral morphology of Dendrobium species.

Figure:

8. D. distichum (0.4X).
9. D. leonis (0.5X).
10. D. leonis (1.2X).
11. D. aggregatum (0.1X).
12. D. aggregatum (1.3X).
13. D. chrysotoxum (0.1X).
14. D. chrysotoxum (1.1X).
15. D. farmeri (0.1X).
16. D. farmeri (1.0X).
17. D. senile (0.3X).
18. D. senile (0.8X).
19. D. trigonopus (0.4X).


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Plate 3. Vegetative and floral morphology of Dendrobium species.

Figure:

20. D. d'albertsii (0.8X).
21. D. d'albertsii (0.1X).
22. D. gouldii (0.5X).
23. D. grantii (1.0X).
24. D. grantii (0.1X).
25. D. mirbellianum (1.0X).
26. D. strebloceras (0.1X).
27. D. stratiotes var. gigantea (0.3X).
28. D. undulatum (0.1X).
29. D. strebloceras (0.7X).
30. D. undulatum (1.0X).

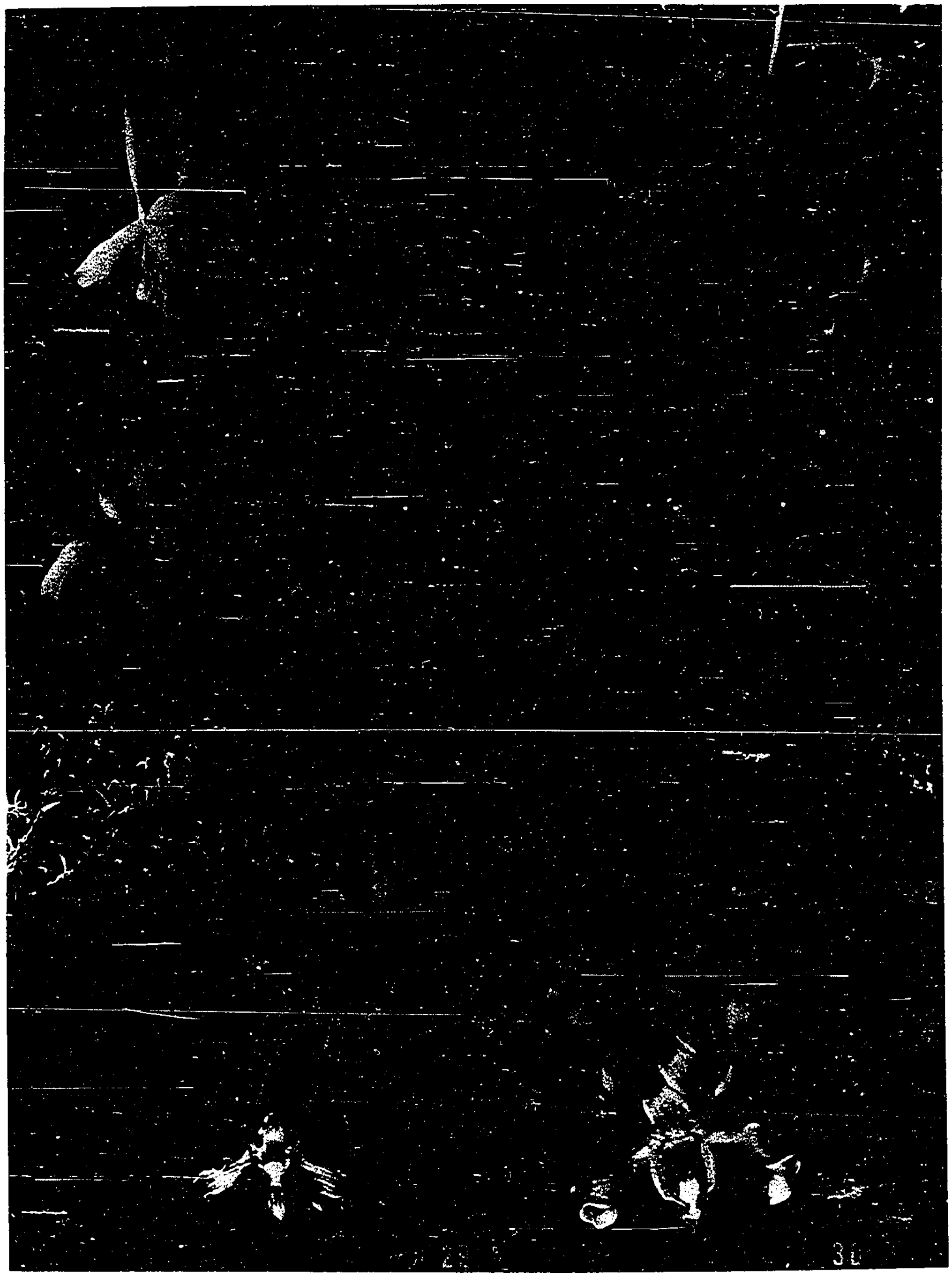
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Plate 4. Vegetative and floral morphology of <u>Dendrobium</u> species.

Figure:

31. D. arachnites (0.4X).
32. D. arachnites (1.2X).
33. D. dixanthum (0.2X).
34. D. dixanthum (1.0X).
35. D. friedericksianum (0.3X).
36. D. friedericksianum (1.0X).
37. D. heterocarpum (0.5X).
38. D. hildebrandii (0.6X).
39. D. hildebrandii (.15X).
40. D. linguella (0.9X).
41. D. lituiflorum (0.7X).
42. D. lituiflorum (.25X).

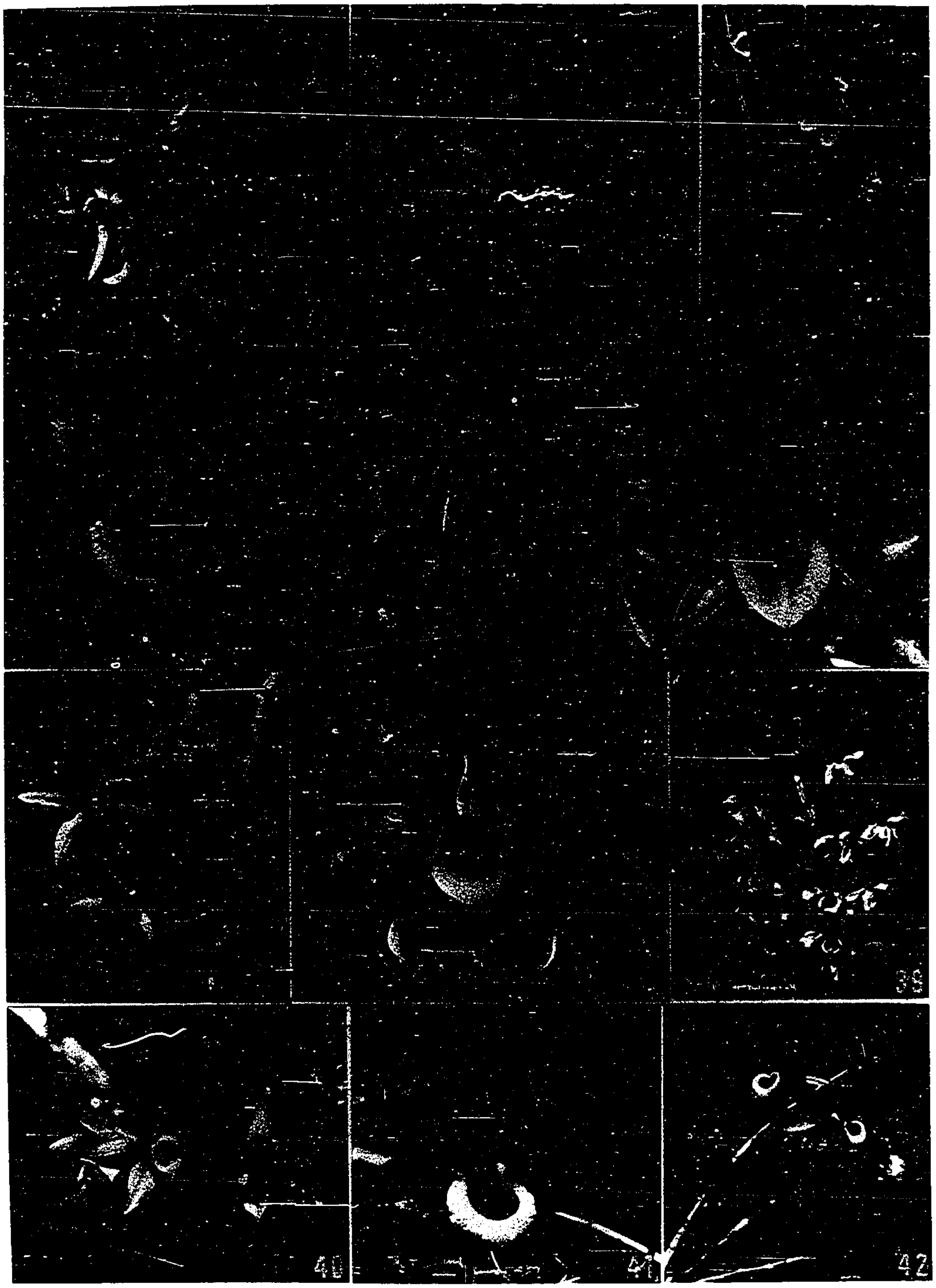

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Plate 5. Vegetative and floral morphology of Dendrobium species.

Figure:

43. D. macrostachyum (0.1X).

44. D. macrostachyum (1.8X).

45. D. monile (0.9X).

46. D. monile (0.2X).

47. D. moschatum (0.3X).

48. D. tortile (0.6X).

49. D. tortile (0.2X).

50. D. primulinum (0.5X).

51. D. primulinum (0.1X).

52. D. parishii (0.2X).

53. D. parishii (0.8X).

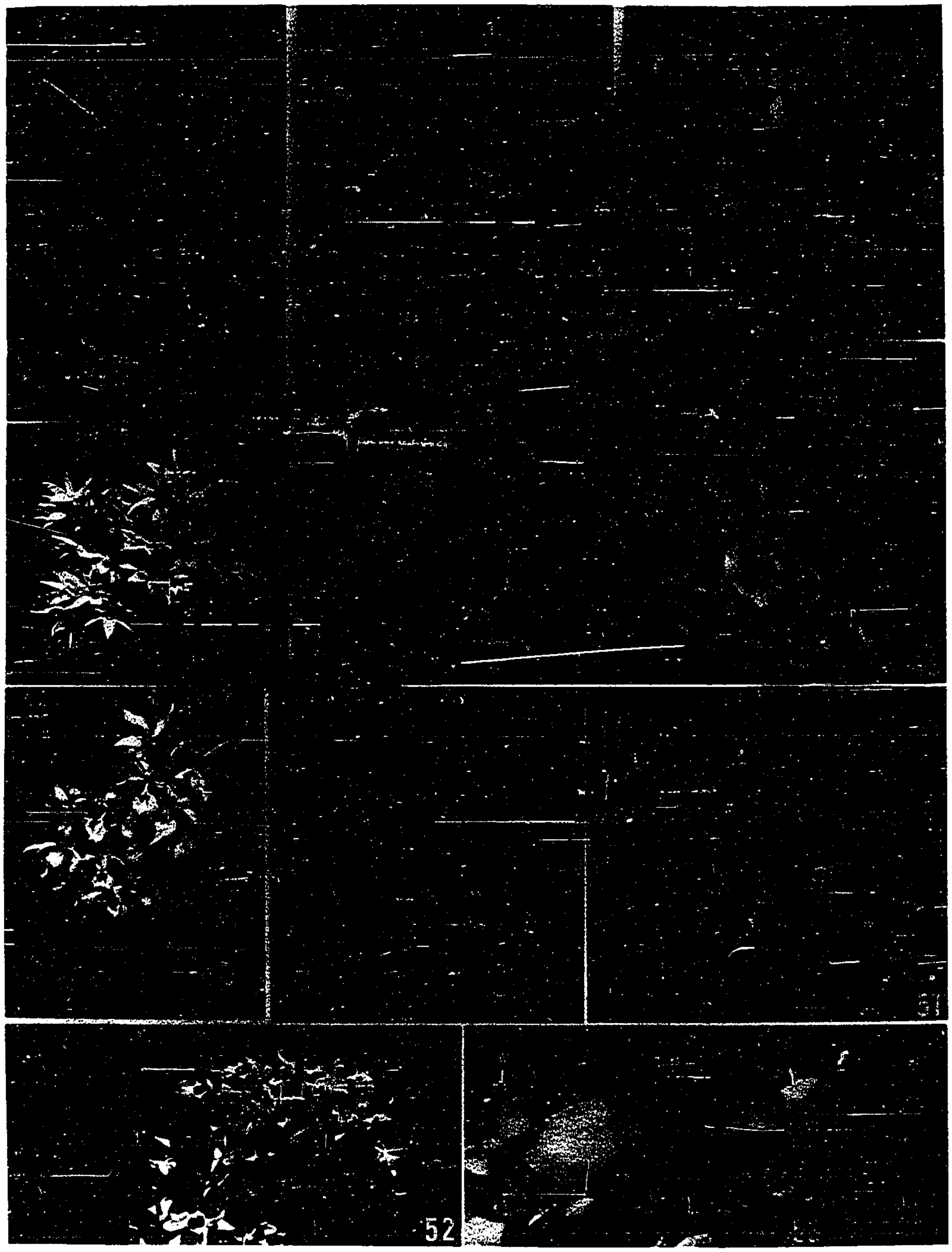

52

Plate 6. Vegetative and floral morphology of <u>Dendrobium</u> species.

Figure:

54. D. macrophyllum (.05X).
55. D. macrophyllum (0.7X).
56. D. spectabile (0.1X).
57. D. spectabile (0.5X).
58. D. canaliculatum (.05X).
59. D. canaliculatum (1.2X).
60. D. sutepense (0.5X).
61. D. cariniferum (0.7X).
62. D. formosum var. giganteum (0.5X).
63. D. draconis (0.6X).
64. D. bellatulum (1.0X).
65. D. delacourii (0.2X).

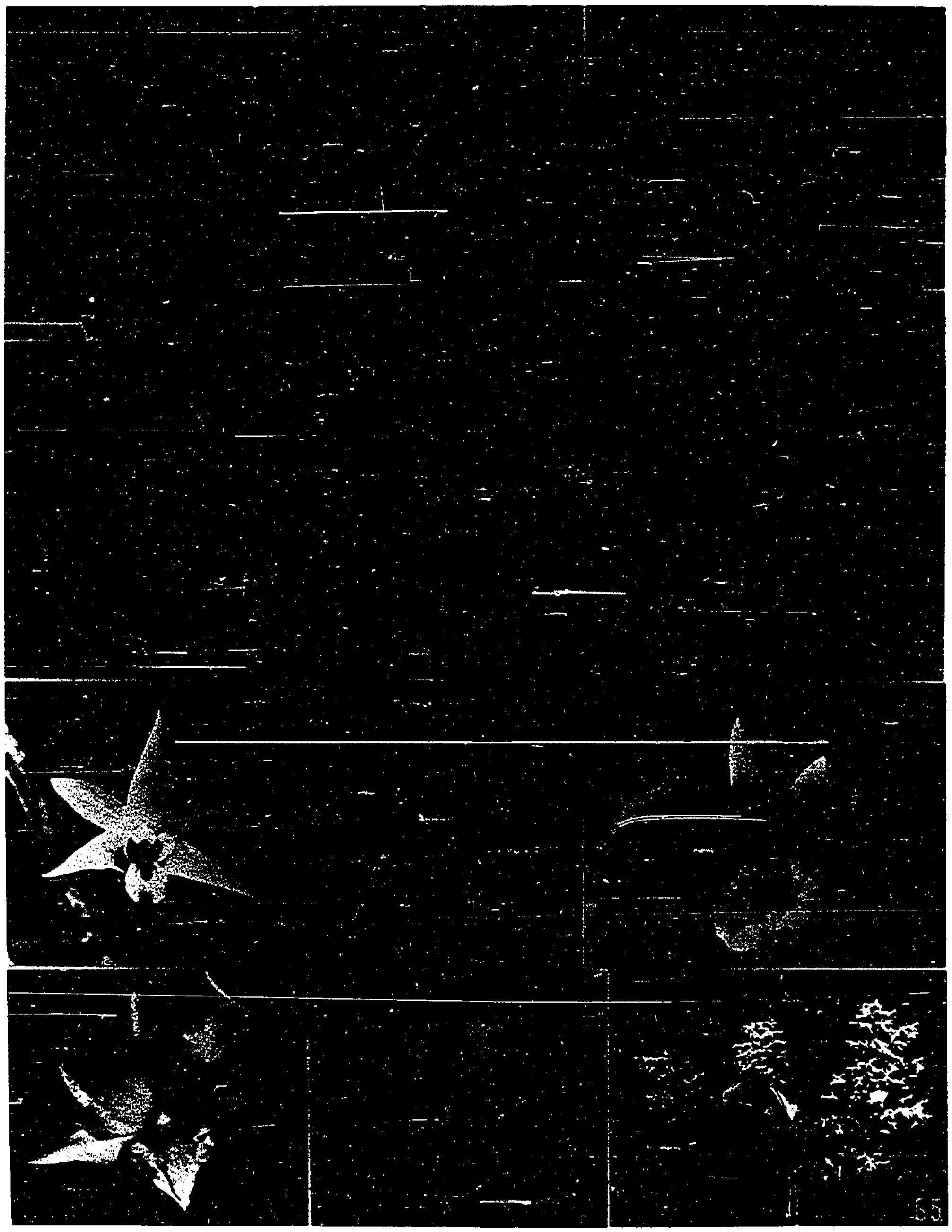

55

Plate 7. Vegetative and floral morphology of Dendrobium species.

Figure:

66. D. bullenianum (3.0X).

67. D. bullenianum (0.3X).

68. D. victoriae-reginae (1.2X).

69. D. victoriae-reginae (.15X).

70. D. biggibum (1.1X).

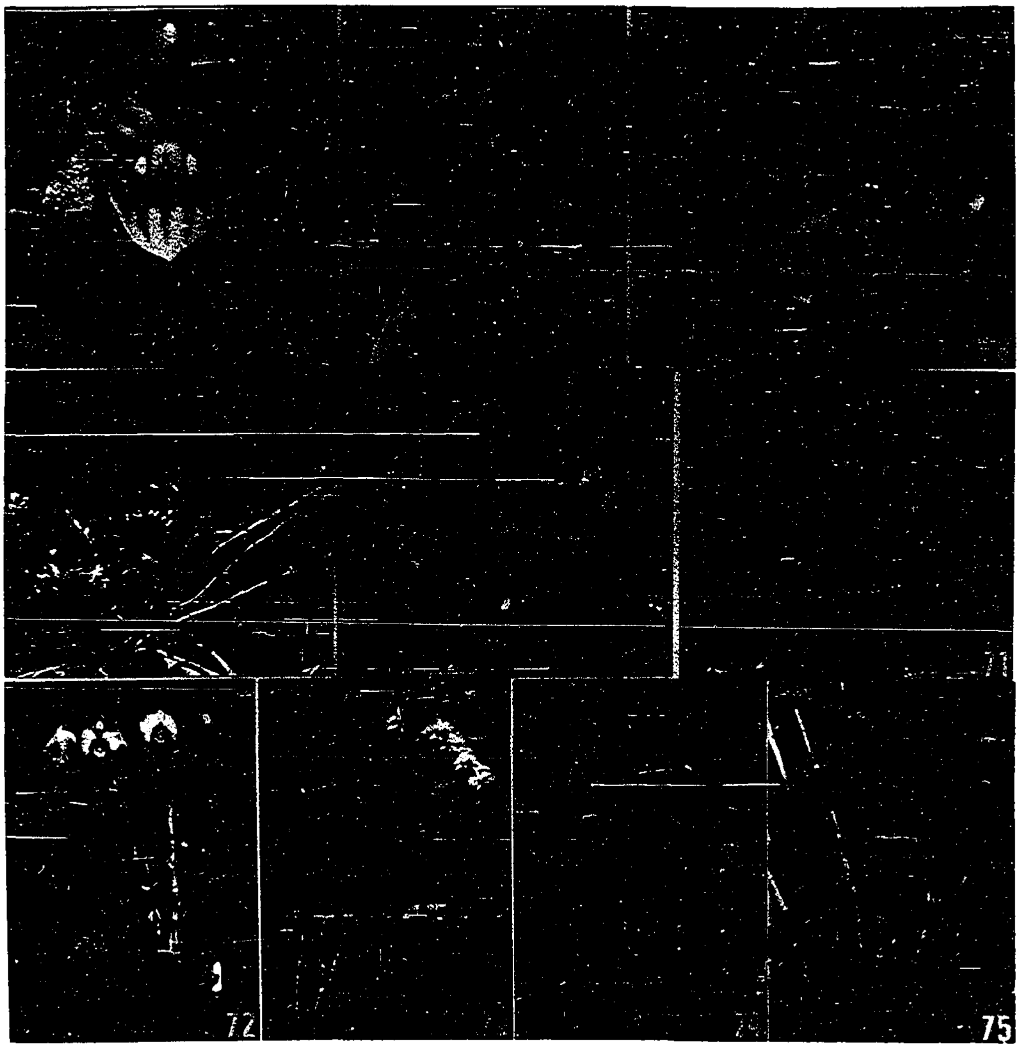
71. D. phalaenopsis (0.6X).

72. D. biggibum (.15X).

73. D. phalaenopsis (.05X).

74. D. crumenatum (.05X).

75. D. crumenatum (.15X).



x Phalaenanthe produced the highest percentage, 79.1%, while Callista x Eugenanthe had the lowest, 3.1%. The remaining 21 combinations which formed fruits ranged from 7.4 to 66.7%. As in the intrasectional crosses, the germination of the seeds showed a relationship similar to that found in the production of pods. Ceratobium x Phalaenanthe gave the highest percentage of viable crosses, 66.7%, while Callista x Eugenanthe produced the lowest, 1.6%. The remaining 18 combinations ranged from 2.2 to 33.3% viable crosses.

Attempts to cross members of the Aporum and Rhopalanthe sections intra- and intersectionally failed. All crosses using D. aggregatum and D. chrysotoxum as female parents failed to produce fruits, although some reciprocal combinations did form fruits and eventually viable seedlings. All selfing and sibling crosses within and between these two species also failed.

A comparison of the production of successful fruits and viable crosses between the Ceratobium and Phalaenanthe sections with the remaining eight sections was tabulated from Tables III and IV. A compatibility scheme based on the differences obtained by crossing the Ceratobium and Phalaenanthe sections with the remaining sections is:

Closer to Ceratobium	Equal or Undetermined	Closer to Phalaenanthe
Pedilonum	Aporum	Eugenanthe
Stachyobium	Callista	Nigrohirsutae
	Latourea	
	Rhopalanthe	

The percentage of non-aborted embryos was determined under microscopic examination (Table V). In the intrasectional crosses, excluding the sibling cross within the Stachyobium section, the range of normal embryos was from 23.6 to 83.3%, with the Latourea x Latourea

Table V. Percentage of normal embryos of *Dendrobium* inter- and intrasectional crosses.

Sections Crossed	Number of Fruits Harvested	Percent Normal Embryos
Callista x Ceratobium	11	0.04
Callista x Eugenanthe	2	42.5
Callista x Latourea	3	0.4
Callista x Nigrohirsutae	1	0.0
Callista x Phalaenanthe	2	0.01
Callista x Stachyobium	1	80.0
Ceratobium x Ceratobium	26	82.0
Ceratobium x Eugenanthe	17	0.02
Ceratobium x Latourea	11	27.8
Ceratobium x Nigrohirsutae	4	0.03
Ceratobium x Pedilonum	2	2.05
Ceratobium x Phalaenanthe	19	84.3
Ceratobium x Stachyobium	4	20.0
Eugenanthe x Eugenanthe	8	51.2
Eugenanthe x Latourea	4	0.01
Eugenanthe x Pedilonum	5	0.01
Eugenanthe x Phalaenanthe	7	0.01
Eugenanthe x Rhopalanthe	2	0.0
Eugenanthe x Stachyobium	2	48.6
Latourea x Latourea	4	83.3
Latourea x Nigrohirsutae	1	20.0
Latourea x Phalaenanthe	2	85.0
Latourea x Stachyobium	1	0.01
Nigrohirsutae x Nigrohirsutae	5	23.6
Nigrohirsutae x Pedilonum	1	0.01
Nigrohirsutae x Phalaenanthe	6	0.01
Phalaenanthe x Phalaenanthe	11	62.8
Phalaenanthe x Stachyobium	1	0.01
Stachyobium x Stachyobium	1	97.0

group exhibiting the highest percentage and the Nigrohirsutae x Nigrohirsutae combination showing the lowest. In the intersectional crosses the range was from 0.0 to 85.0%, with Latourea x Phalaenanthe and Ceratobium x Phalaenanthe producing the highest percentage of non-aborted embryos. A scheme based on the differences in the percentage of normal embryos in sections crossed with the Ceratobium and Phalaenanthe sections is:

Closer to Ceratobium	Equal or Undetermined	Closer to Phalaenanthe
Pedilonum	Aporum	Latourea
Stachyobium	Callista	
	Eugenanthe	
	Nigrohirsutae	
	Rhopalanthe	

The two classification schemes are in general agreement with one another. When the information from the two schemes is incorporated, the relationship is:

Closer to Ceratobium	Equal or Undetermined	Closer to Phalaenanthe
Pedilonum	Aporum	Eugenanthe
Stachyobium	Callista	Latourea
	Rhopalanthe	Nigrohirsutae

The compatibility relationship between Callista x Stachyobium and Callista x Eugenanthe is about equal, based on one successful hybrid in each case. The relationship of Latourea to Nigrohirsutae is closer than to Pedilonum or Stachyobium, with 20% normal embryos produced in the former cross and less than 0.01% in the latter two. It appears that the relationship shown agrees among the sections in each grouping on the basis of percentage of non-aborted embryos in the intersectional hybrids. The compatibility relationship shown above does not completely agree with data published on registered hybrids and previous genome studies.

During the past century 248 Dendrobium primary hybrids have been recorded (Sander, 1946; Sander and Wreford, 1961; Royal Horticultural Society, 1964; Dillon, 1965-1967). These hybrids are listed in alphabetical order in Appendix A and by parentage in Appendix B. Nine of Schlechter's (1912) sections are represented in 22 combinations (Appendix C). Seven of the combinations are intrasectional while the remaining 15 are intersectional. Fifty percent of the total hybrids are in either the Eugenanthe x Eugenanthe or Ceratobium x Ceratobium groups. The greatest number of intersectional hybrids is found in the Ceratobium x Phalaenanthe combination, where 53 hybrids have been recorded. These three combinations represent 71% of all the Dendrobium primary hybrids recorded. The remainder of the intrasectional hybrids comprise 15% of the total and the intersectional hybrids only 14%.

The registration of Dendrobium hybrids is generally based on two criteria. Hybrids registered are usually only those considered to have some horticultural merit and these registrations probably represent only a highly selected sampling of actual hybrids. Secondly, availability of the parental species determines the production of the hybrids. The data from the published crosses are not sufficient to show definite compatibility relationships between the sections although there is an indication that members of the Ceratobium and Phalaenanthe sections are compatible with one another. The data also indicate that the members of the Eugenanthe section, which includes the greatest number of species, are sexually compatible among themselves but not highly compatible with species in other sections. Too few crosses among the remaining six sections have been recorded to show any definite compatibility relationships.

The information gathered from all of the registered crosses indicated that the members of the Eugenanthe section were relatively compatible with one another although the results of the present study indicate that there was a relatively low compatibility relationship among species in this section. Of all the intrasectional combinations which produced any hybrids, Eugenanthe had the lowest percentage of successful crosses per pollination, 4.5%. The discrepancy in the data from the two studies might be explained by the large number of species in the Eugenanthe section and the length of time they have been in cultivation. The members of the Eugenanthe section were the first to be cultivated in Europe and many of these have been grown for a century or more (Holttum, 1957). Even with a conservative estimate of 400 species in this section, hundreds of combinations between species could have been made during the last century and the registered 63 primary hybrids could represent a very small percentage of actual pollinations.

The list of registered crosses (Appendix C) shows five crosses of Latourea x Ceratobium and only four for Latourea x Phalaenanthe. This small difference might be attributed to the greater number of species in the Ceratobium section which might be crossed with the Latourea group. The remainder of the data found in this table was not sufficient to either agree or disagree with the results of the present study.

The work of Kamemoto, Shindo, and Kosaki (1964) on genome relationships in *Dendrobium* indicates that Latourea is more closely related to Ceratobium than to Phalaenanthe. A hybrid studied of Latourea x Ceratobium had a mean of 10.8 bivalents while a hybrid of Latourea x Phalaenanthe exhibited an average of only 1.8 bivalents. This information indicated that the compatibility scheme earlier devised may be in error by showing the Latourea section closer to the Phalaenanthe than the Ceratobium group.

In all the previously reported combinations of the Dendrobium sections, only the Callista x Callista cross and those involving the Dendrocoryne and Eleutheroglossum sections were not reproduced in this research. In addition, eight new combinations were made:

Callista x Latourea	Eugenanthe x Stachyobium
Callista x Stachyobium	Latourea x Nigrohirsutae
Ceratobium x Pedilonum	Latourea x Stachyobium
Ceratobium x Stachyobium	Nigrohirsutae x Pedilonum

The separation of all the Dendrobium species examined in this research into Schlechter's sections based on external morphology does not appear to be reflected in their crossability. In many instances species cross as readily among sections as within the same section. An example is the Eugenanthe section, which produced only 4.5% viable crosses per pollination intrasectionally but when crossed with the Ceratobium, Phalaenanthe, and Pedilonum sections, the percentages of viable crosses were 6.2, 9.1, and 11.8 respectively (Table IV). The percentage of normal embryos in the harvested fruits was also not a distinguishing factor, especially in Ceratobium x Ceratobium as compared to Ceratobium x Phalaenanthe (Table V).

Karyotype Relationships

The chromosome numbers of 33 Dendrobium species, representative of 11 of Schlechter's 41 sections, were determined by microscopic examination (Table VI). Thirty-one of the species had a somatic number of 38, and two, *D. leonis* (Figs. 9-10, 77, 100) and *D. dixanthum* (Figs. 33-34), were 2n=40. The chromosome complements of five species

Table VI. Chromosome numbers of Dendrobium species.

Section and Species	Present Count 2n	Previous Counts 2n	n	Authority
Aporum				
distichum	38	57		Vaj. & Ran. '60
		38		Pancho '65
leonis	40			
Callista				
aggregatum	38	38	19	Vaj. & Ran. '60
		38	19	Kos. & Kam. '61
		32-35		Chardard '63
		38		Kam. & Sag. '67
chrysotoxum	38		20	Hoffmann '30
		40		Ito & Mut. '57
		38		Kos. & Kam. '61
		38		Jones '63
		40		Chardard '63
		38		Tanaka '64
		38		Kam. & Sag. '67
trigonopus	38			
Ceratobium				
d'albertsii	38	38	19	Kos. & Kam. '61
gouldii	38	38		Kosaki '58
		38		Kos. & Kam. '61
grantii	38	38		Kosaki '58
		38		Kos. & Kam. '61
mirbellianum	38			
stratiotes	38	38		Kosaki '58
		38		Vaj. & Ran. '60
		38		Kos. & Kam. '61
		38		Jones '63
strebloceras	38	38		Jones '63
undulatum	38	38	19	Kos. & Kam. '61
(discolor)		38		Jones '63
Eleutheroglossum				
canaliculatum	38	2x		Jones '63

Table VI. (Continued) Chromosome numbers of Dendrobium species.

Section and Species	Present Count 2n	Previous Counts 2n	n	Authority
Eugenanthe				
anosmum	38	40		Eftimiu-Heim '41
(superbum)		40		Ito & Mut. '57
			19	Kosaki '58
			19	Vaj. & Ran. '60
			19	Kos. & Kam. '61
arachnites	38	38		Pancho '65
dixanthum	40	41		Jones '63
		40		Kam. & Sag. '67
heterocarpum	38	38		Kosaki '58
(aureum)		38		Jones '63
		38		Pancho '65
		38		Kam. & Sag. '67
linguella (hercoglossum)	38	38		Kam. & Sag. '67
macrostachyum	38	38		Jones '63
monile	38	38		Miduno '40
		38		Ito & Mut. '57
		38		Mut. & Naka. '58
		38		Kos. & Kam. '61
		38		Jones '63
		38+1+3f		Jones '63
moschatum	38	40		Jones '63
		38		Chardard '63
		38		Kam. & Sag. '67
		39		Kam. & Sag. '67
senile	38	38		Kam. & Sag. '67
tortile	38	38		Kos. & Kam. '61
		38		Jones '63
		38		Kam. & Sag. '67
Latourea				
macrophyllum	38	38		Kosaki '58
		38		Kos. & Kam. '61
spectabile	38	38		Kosaki '58
		38		Kos. & Kam. '61

Table VI. (Continued) Chromosome numbers of Dendrobium species.

Section and Species	Present Count 2n	Previous Counts 2n	n	Authority
Nigrohirsutae				
draconis	38	38		Kos. & Kam. '61
		38		Kam. & Sag. '67
formosum var. giganteum	38	38		Kos. & Kam. '61
		38		Kos. & Sag. '67
Pedilonum				
bullenianum	38			
victoriae-reginae	38	38		Jones '63
Phalaenanthe				
biggibum	38	38		Jones '63
phalaenopsis	38	38		Kosaki '58
		38	19	Kos. & Kam. '61
Rhopalanthe				
crumenatum	38	38+1f		Jones '63
		40		Pancho '65
		38		Kam. & Sag. '67
Stachyobium				
delacourii (ciliatum)	38	38		Kam. & Sag. '67

have not previously been reported. These are: D. leonis, 2n=40; D. trigonopus (Figs. 19, 79, 102), 2n=38; D. canaliculatum (Figs. 58-59, 83, 106), 2n=38; D. bullenianum (Figs. 66-67), 2n=38; and D. mirbellianum (Fig. 25), 2n=38.

The information obtained from this study and that tabulated by Tanaka and Kamemoto (1963, 1964) indicate that a diploid number of both 38 and 40 is found in the sections Aporum, Callista, Eugenanthe, Nigrohirsutae, Pedilonum, and Rhopalanthe. A constant somatic number of 38 has been recorded in the sections Ceratobium, Eleutheroglossum, Latourea, and Stachyobium. In the Phalaenanthe section somatic numbers of 38, 57, and 76 have been reported by various researchers (Kosaki, 1958; Kosaki and Kamemoto, 1961) although the polyploids may be horticultural variants. It is not known if the ancestral species of Dendrobium were 2n=38 or 2n=40 with the remaining somatic number arising as a balanced aneuploid or were of some entirely different combination.

Earlier studies on chromosome numbers in Dendrobium have indicated 2n=40 as the common number (Hoffmann, 1930; Eftimiu-Heim, 1941; Ito and Mutsuura, 1957) but the more recent reports, tabulated by Tanaka and Kamemoto (1963, 1964) show that 2n=38 predominates. It might be presumed that 2n=38, which is the preponderate number, is the more primitive form in Dendrobium, although evolution of the karyotype might have proceeded in either direction (Stebbins, 1950).

A few Dendrobium species have been reported to have both 2n=38 and 2n=40. Whether this actually occurs in nature or is a result of misinterpretation of the chromosome configuration is difficult to decide. Since the more recent counts generally confirm a 2n=38 for many of the species which previously had been counted as both 2n=38 and 2n=40, it is reasonable to assume that many of the earlier counts were in error. Centric fragments of minute size were found in three Dendrobium species by Jones (1963), of which one species was D. monile. In the present study it was observed that D. monile (Figs. 88, 111) has one pair of chromosomes with very large satellites. These satellite bodies are often loosely attached to the parental chromosome and at some distance from it or they may be broken off completely. Misinterpretation of the metaphase configuration might regard these either as separate chromosomes or fragments (B-chromosomes). If these were considered separate chromosomes by previous researchers, a transition in the number reported from 2n=38 to 2n=40 would be relatively simple. Not all of the cases may be explained in this manner. Kosaki and Kamemoto (1961) clearly showed three fragment chromosomes in D. moschatum var. cupreum and Kamemoto and Sagarik (1967) found one plant of D. moschatum which had a somatic number of 39 while four other plants of the same species were 2n=38. Further studies on the remaining Dendrobium species which have not been cytologically examined including intense research on those that have been studied should help clarify which is the most primitive form, 2n=38 or 2n=40, and whether or not deviations in somatic number within a species does exist in nature.

Detailed examinations of chromosome morphology were made of 23 Dendrobium species in 11 sections (Table VII; Figs. 76-121). Mean chromosome size, on the basis of chromosome length, varied within species from 14.0 $\pm$ 0.2 to 27.6 $\pm$ 1.2, where one unit equals 0.091 microns. The smallest chromosome set was of D. distichum (Figs. 8, 76, 99) in the Aporum section and the largest was of D. anosmum (Figs.

Table VII. Karyotype analysis of species of Dendrobium.

Species	Number of Cells Observed	Mean Chromosome Length*	Mean of Smallest Chromosome	Mean of Largest Chromosome	Mean S%
Aporum					
distichum	3	14.0 ± 0.2	9.3 ± 0.6	20.3 ± 1.5	46.1 ± 4.6
leonis	3	17.8 ± 1.4	14.0 ± 1.0	24.3 ± 3.8	58.3 ± 5.3
Callista					
aggregatum	3	15.8 ± 0.4	11.3 ± 0.6	22.3 ± 2.1	50.9 ± 3.7
trigonopus	2	18.6 ± 0.4	12.5 ± 0.5	29.0 ± 2.0	43.2 ± 1.8
Ceratobium					
gouldii	3	16.3 ± 0.4	9.7 ± 1.2	27.3 ± 2.1	35.3 ± 2.2
grantii	3	16.9 ± 1.6	10.7 ± 1.1	23.3 ± 1.1	45.7 ± 4.1
undulatum	3	16.9 ± 0.8	9.3 ± 0.6	31.7 ± 2.5	29.5 ± 1.4
Eleutheroglossum					
canaliculatum	3	21.2 ± 0.5	16.7 ± 1.2	33.0 ± 1.0	50.5 ± 3.5
Eugenanthe					
anosmum	3	27.6 ± 1.2	21.3 ± 2.1	45.3 ± 4.7	47.1 ± 0.4
arachnites	3	20.2 ± 0.8	13.7 ± 0.6	26.3 ± 2.5	52.0 ± 2.1
heterocarpum	3	17.8 ± 0.9	13.3 ± 0.6	24.7 ± 1.1	54.2 ± 4.2
linguella	3	15.2 ± 0.6	10.7 ± 1.1	24.3 ± 1.5	43.8 ± 2.3
monile	3	15.7 ± 0.6	11.3 ± 0.6	22.7 ± 2.1	50.1 ± 2.2
moschatum	3	18.6 ± 0.6	15.0 ± 1.0	26.7 ± 1.5	56.3 ± 4.1

*Length of chromosomes measured at 5500X, using 0.5 mm. as the unit.

Table VII. (Continued) Karyotype analysis of species of Dendrobium.

Species	Number of Cells Observed	Mean Chromosome Length	Mean of Smallest Chromosome	Mean of Largest Chromosome	Mean S%
Latourea					
macrophyllum	3	20.7 ± 1.8	14.0 ± 1.0	29.7 ± 4.0	47.5 ± 3.0
Nigrohirsutae					
draconis	3	24.0 ± 0.3	15.7 ± 0.6	32.0 ± 2.0	49.0 ± 1.7
formosum var. giganteum	3	25.1 ± 0.9	16.7 ± 0.6	33.3 ± 2.5	50.1 ± 2.5
sutepense	2	22.0 ± 0.6	13.5 ± 0.5	31.5 ± 0.5	42.9 ± 3.2
Pedilonum					
victoriae-reginae	3	16.8 ± 0.6	12.7 ± 0.6	22.7 ± 1.5	40.5 ± 2.5
Phalaenanthe					
biggibum	3	17.8 ± 0.5	11.3 ± 1.5	24.0 ± 1.7	47.1 ± 3.3
phalaenopsis	3	16.2 ± 0.6	11.0 ± 0.0	26.3 ± 1.5	41.9 ± 2.4
Rhopalanthe					
crumenatum	2	16.2 ± 0.6	9.0 ± 0.0	24.0 ± 1.5	37.6 ± 2.2
Stachyobium					
delacourii	3	18.0 ± 1.1	12.3 ± 1.1	25.7 ± 2.1	48.1 ± 3.4

Table VII. (Continued) Karyotype analysis of species of Dendrobium.

Species	Mean Number of Chromosomes with F% 0-30.0	30.1-45.0	45.1-50.0	Mean F%
Aporum				
distichum	0.0	21.3 ± 1.5	16.7 ± 1.5	43.8 ± 0.6
leonis	0.0	17.3 ± 2.1	22.7 ± 2.1	44.8 ± 0.7
Callista				
aggregatum	0.0	16.7 ± 1.1	21.3 ± 1.1	44.8 ± 0.6
trigonopus	0.0	23.0 ± 1.0	15.0 ± 1.0	41.9 ± 0.5
Ceratobium				
gouldii	4.0 ± 0.0	19.0 ± 2.6	15.0 ± 2.6	41.3 ± 0.6
grantii	0.0	24.7 ± 2.3	13.3 ± 2.3	43.0 ± 0.8
undulatum	2.0 ± 0.0	20.7 ± 3.5	15.3 ± 3.5	41.5 ± 1.2
Eleutheroglossum				
canaliculatum	2.0 ± 0.0	28.3 ± 1.5	7.7 ± 1.5	41.0 ± 0.9
Eugenanthe				
anosmum	0.0	29.0 ± 2.7	9.0 ± 2.7	41.9 ± 0.8
arachnites	0.0	23.7 ± 0.6	14.3 ± 0.6	41.7 ± 0.4
heterocarpum	0.0	16.7 ± 3.5	21.3 ± 3.5	45.0 ± 1.3
linguella	0.0	15.7 ± 1.1	22.3 ± 1.1	45.1 ± 0.4
monile	0.0	21.7 ± 2.1	16.3 ± 2.1	44.3 ± 0.6
moschatum	0.0	22.7 ± 1.5	15.3 ± 1.5	43.6 ± 1.6

Table VII. (Continued) Karyotype analysis of species of Dendrobium.

Species	Mean Number of Chromosomes with F%			Mean F%
	0-30.0	30.1-45.0	45.1-50.0	
Latourea				
macrophyllum	0.0	24.3 ± 2.0	13.7 ± 2.0	43.3 ± 0.4
Nigrohirsutae				
draconis	0.0	24.3 ± 2.1	13.7 ± 2.1	42.3 ± 0.9
formosum var. giganteum	0.0	26.0 ± 3.0	12.0 ± 3.0	42.4 ± 1.0
sutepense	0.0	28.5 ± 1.5	9.5 ± 1.5	41.0 ± 0.9
Pedilonum				
victoriae-reginae	0.0	19.3 ± 1.1	18.7 ± 1.1	44.0 ± 0.5
Phalaenanthe				
biggibum	0.0	21.3 ± 2.5	16.7 ± 2.5	42.9 ± 0.6
phalaenopsis	6.0 ± 0.0	21.7 ± 1.5	10.3 ± 1.5	39.7 ± 0.2
Rhopalanthe				
crumenatum	0.0	26.5 ± 2.1	11.5 ± 2.1	41.7 ± 0.6
Stachyobium				
delacourii	0.0	20.0 ± 2.6	18.0 ± 2.6	44.8 ± 0.5

Plate 8. Somatic chromosomes of Dendrobium species which were used in the karyotype analyses (1800X).

Figure:

76. D. distichum.

77. D. leonis.

78. D. aggregatum.

79. D. trigonopus.

80. D. grantii.

81. D. undulatum.

82. D. gouldii.

83. D. canaliculatum.

84. D. anosmum (superbum).

85. D. arachnites.

86. D. heterocarpum (aureum).

87. D. linguella (hercoglossum).

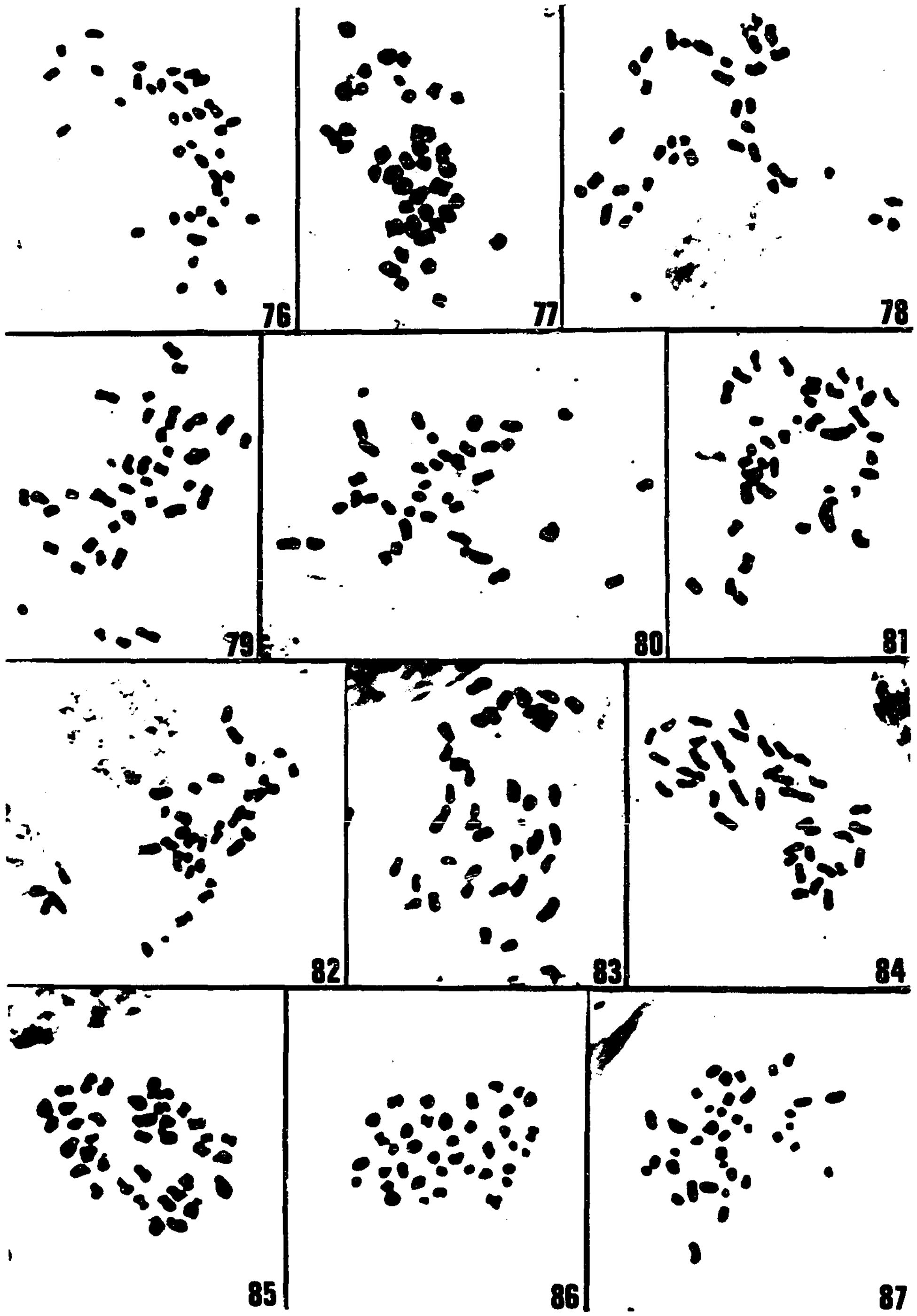

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Plate 9. Somatic chromosomes of Dendrobium species which were used in the karyotype analyses (1800X).

Figure:

88. D. monile.

89. D. moschatum.

90. D. macrophyllum.

91. D. draconis.

92. D. formosum var. giganteum.

93. D. sutepense.

94. D. victoriae-reginae.

95. D. biggibum.

96. D. phalaenopsis.

97. D. crumenatum.

98. D. delacourii.

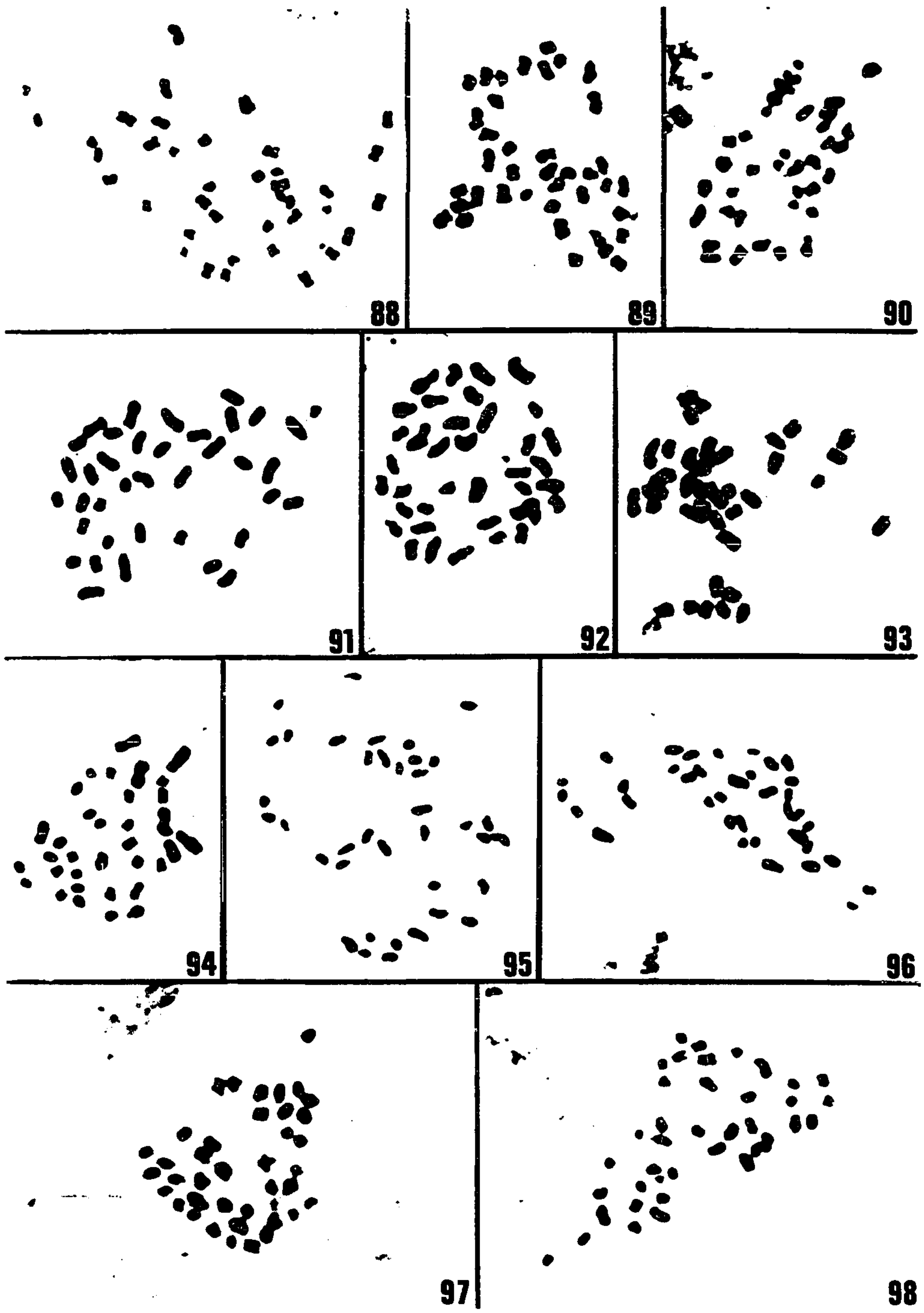
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Plate 10. Karyotypes of Dendrobium species. (3300X).

Figure:

99. D. distichum.

100. D. leonis.

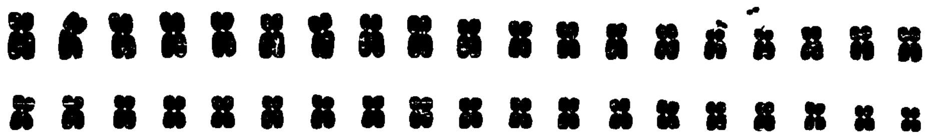
101. D. aggregatum.

102. D. trigonopus.

103. D. gouldii.

104. D. grantii.

99



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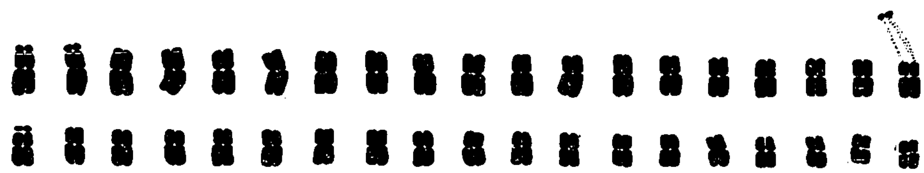

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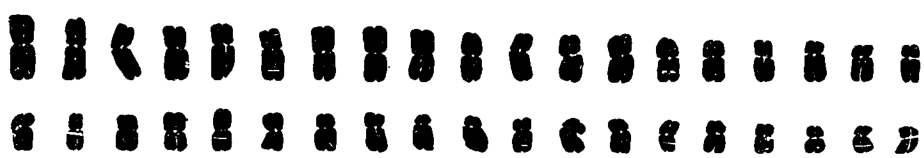

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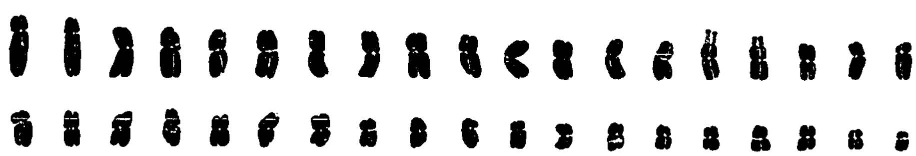

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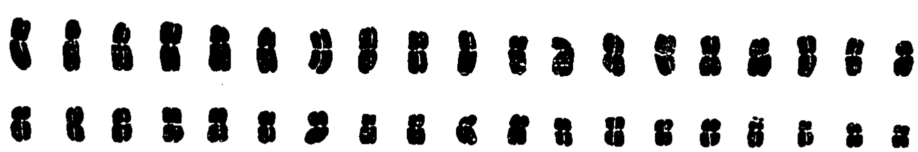


Plate 11. Karyotypes of Dendrobium species. (3300X).

Figure:

105. D. undulatum.

106. D. canaliculatum.

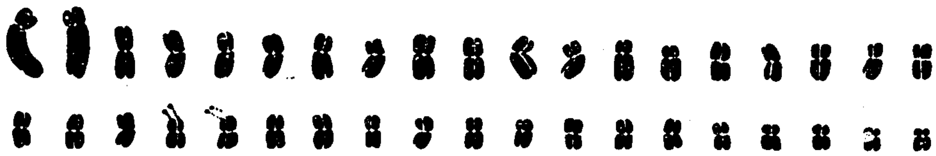
107. D. anosmum (superbum).

108. D. archnites.

109. D. linguella (hercoglossum).

110. D. heterocarpum (aureum).

105



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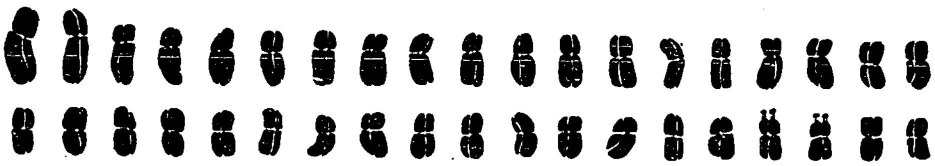

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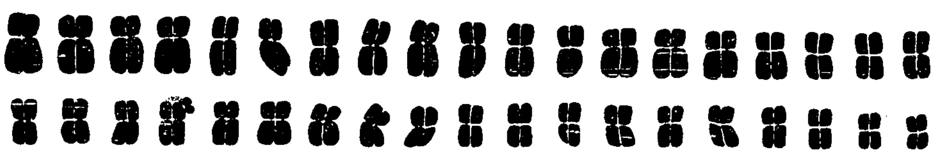

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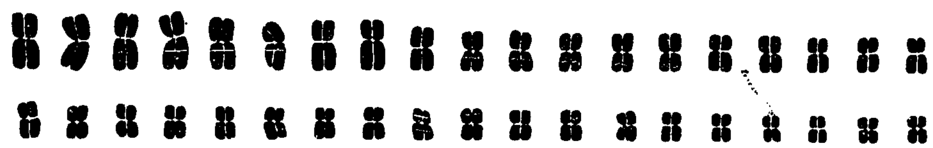

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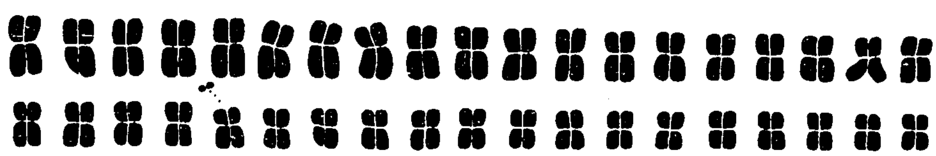


Plate 12. Karyotypes of Dendrobium species (3300X).

Figure:

111. D. monile.

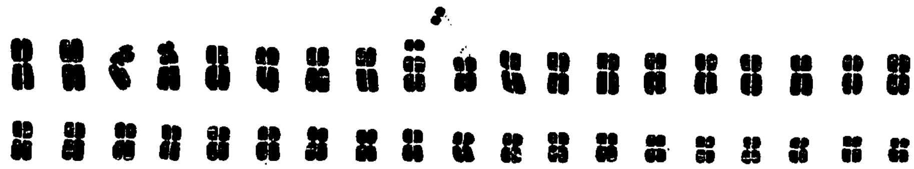
112. D. moschatum.

113. D. macrophyllum.

114. D. draconis.

115. D. formosum var. giganteum.

116. D. sutepense.

111


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113


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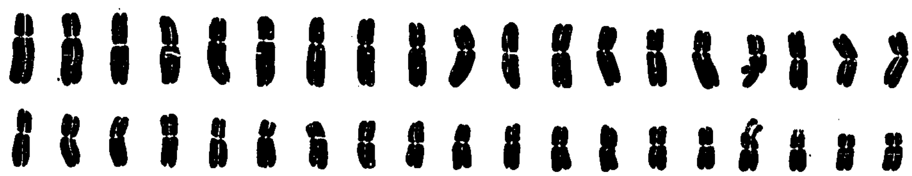

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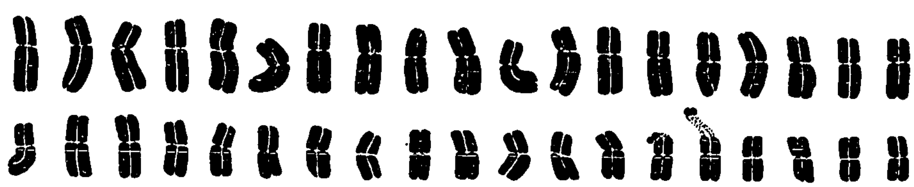

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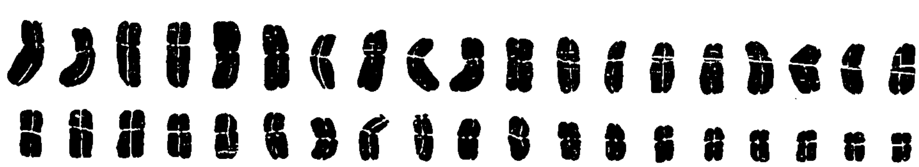

Plate 13. Karyotypes of Dendrobium species (3300X).

Figure:

117. D. victoriae-reginae.

118. D. biggibum.

119. D. phalaenopsis.

120. D. crumenatum.

121. D. delacourii.

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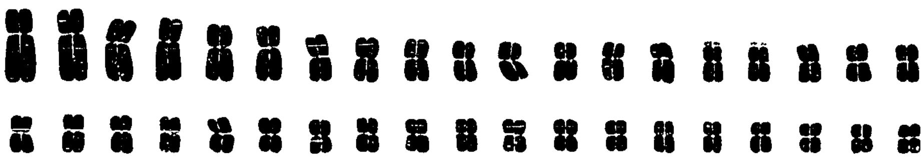

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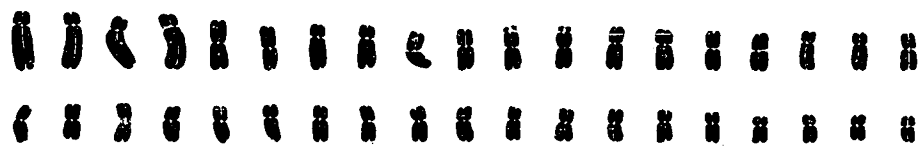

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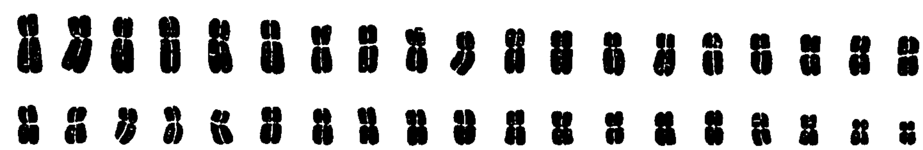

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84, 107) in the Eugenanthe group. The average mean chromosome lengths of each section studied, arranged in descending order, were: Nigrohirsutae, 23.7; Eleutheroglossum, 21.2; Latourea, 20.7; Eugenanthe, 19.2; Stachyobium, 18.0; Callista, 17.2; Phalaenanthe, 17.0; Pedilonum, 16.8; Ceratobium, 16.7; Rhopalanthe, 16.2; and Aporum, 15.9.

Although many species exhibited definite differences in mean chromosome size, the sections cannot be distinguished by the average chromosome length of their constituents. There was almost as much variation in the mean chromosome size within some of the sections as between all of the sections. A maximum difference, including standard deviation, between all of the species examined was 15.0 units. In the Eugenanthe section alone, the species with the smallest chromosome complement, D. linguella (Figs. 40, 87, 109), and that with the largest chromosome set, D. anosmum, showed a maximum difference of 14.2 units. It must be revealed that this was the only section that showed such a wide variation in mean chromosome size of the individual species, but with such a wide variation in one section, comparisons between sections are meaningless.

Unlike the study on Phalaenopsis by Shindo and Kamemoto (1963e) where a relationship was shown between average chromosome size and the taxonomic sections of the genus, no such definite relationship was evident in Dendrobium. Even though all the sections could not be distinguished by mean chromosome length, it was possible to detect differences among some of the sections. With the exception of D. anosmum in the Eugenanthe section, the species in the Nigrohirsutae group had the largest chromosomes and could easily be separated from the species in all but three of the other sections.

Stebbins (1950) observed that phylogenetic reduction and phylogenetic increase in chromosome lengths are about equally common and that both of these processes are reversible. In some of the genera studied there was a difference in geographic distribution between species with larger chromosomes and those with smaller chromosomes, with the species having larger chromosomes occupying cooler climates than those with smaller ones. In about half of the plant groups studied no differences existed.

The range in the geographic distribution of the Dendrobium species within each section studied is too diverse to generalize on a relationship between chromosome size and climatic habitats. In the Nigrohirsutae section, which exhibited the largest average chromosomes, species are found in the cool highlands of the Philippines and the warm lowlands of Thailand. These are two quite different climatic areas. Similar differences are found within the Eugenanthe section, which has both large and small chromosome species occupying similar climatic zones. No relationship was found between chromosome size and geographical and climatological distribution in the 23 species studied.

The species showed a range in the mean S%, which is one measure of the symmetry of the chromosome complement, from 29.5 $\pm$ 1.4 to 58.3 $\pm$ 5.3 (Table VII). The two species at either end of the range were D. undulatum (Figs. 28, 30, 81, 105) and D. leonis (Figs. 77, 100), respectively. The averages of the mean S% of each section studied, arranged in ascending order, were: Ceratobium, 36.8; Rhopalanthe, 37.6; Pedilonum, 40.5; Phalaenanthe, 44.5; Callista, 47.1; Nigrohirsutae, 47.3; Stachyobium, 48.1; Eleutheroglossum, 50.5; Eugenanthe, 50.6; and Aporum, 52.2.

Dendrobium leonis had very uniform, medium sized chromosomes with a difference of only 10.3 units between the largest and the smallest chromosomes. In comparison, D. undulatum exhibited a difference of 22.4 units, over twice that found in the most symmetrical species. The very low S% characterized by D. undulatum, D. gouldii (Figs. 22, 82, 103), and D. phalaenopsis (Figs. 71, 73, 96, 119) was produced by the presence of either two, four, or six large subterminal chromosomes accompanied by exceedingly small median to submedian chromosomes. The karyotype of D. undulatum was distinguishable from all the other species which were examined by the existence of one pair of very large, heterochromatic, subterminal chromosomes accompanied with very small chromosomes. As observed with the average chromosome size differences in the species and sections, it was not possible to distinguish individual sections on the basis of S%, but some species were detected by S% in conjunction with other morphological characteristics of the karyotypes.

Plants with asymmetrical karyotypes are usually specialized morphologically, either in vegetative parts, or flowers and fruits, or any combination of these three (Stebbins, 1950). Since the species studied were all in the genus Dendrobium with similar floral morphology, only differences in vegetative morphology and inflorescence habit could be compared. Several morphological characteristics have been shown to be highly specialized and advanced by various researchers, generalizing on the plant kingdom (Dobzhansky, 1947; Holttum, 1958; Dressler and Dodson, 1960). A few of these features are:

Primitive	Advanced
leaves herbaceous	leaves thick, fleshy
evergreen	deciduous
upright growth	climbing or pendulous
short internodes	long internodes
single-flowered inflorescence	multiple-flowered inflorescence

An attempt was made to correlate some of these characteristics with the average S% in a few of the species examined. No relationship was shown between these morphological features and the average S% of the sections, since no significant differences in mean S% between all the sections was observed. There were differences in the average S% of a few species and some of these species were studied.

Dendrobium undulatum, which has the most asymmetrical karyotype on the basis of S%, is characterized by having the primitive features of herbaceous leaves, an evergreen habit, and an upright growth. It also has the advanced features of long internodes and a multiple-flowered inflorescence. Both primitive and advanced features are exhibited by this species and no positive relationship can be shown to exist between the advanced karyotype and advanced vegetative characters.

The species with one of the most primitive karyotypes, D. leonis, possesses the advanced feature of fleshy leaves. Its primitive features include short internodes, an evergreen habit, upright growth, and a single-flowered inflorescence. It appears that the lack of vegetative specialization, at least in the features discussed, is exemplified by the primitive, symmetrical karyotype.

Dendrobium heterocarpum (Figs. 86, 100), whose karyotype is not significantly different from that of D. leonis on the basis of S%, has many advanced features. Some of these advanced features are long internodes, pendulant growth, a deciduous habit, and a multiple-flowered inflorescence. The vegetative characters of this species do not reflect the primitiveness of the karyotype. The evolution of the karyotypes of all of the sections examined is not reflected in the external morphological specializations of their constituents on the basis of mean S%, although a few of the species show what appears to be a valid correlation.

The mean F%, which is another method of measuring the symmetry of the karyotype based on the position of the centromere, varied from that of D. phalaenopsis, 39.7 ± 0.2, to that of D. linguella (Figs. 87, 109), 45.1 ± 0.4 (Table VII). These are in the Phalaenanthe and Eugenanthe sections, respectively. The differences in the averages of the mean F% of the sections are not significant among all the sections. It was not possible to separate the sections on the basis of average F%, although a few of the species exhibited significant differences in F%.

Dendrobium phalaenopsis showed a significant difference in mean F% from all of the other species examined, including D. biggibum (Figs. 95, 118), which is in the same Phalaenanthe section. Even though a significant difference in mean F% was shown to exist between species in different sections, just as much variation was shown between species in the same section.

Karyotype symmetry with particular reference to the position of the centromere appeared to be a valuable characteristic that has been shown to be correlated with the evolution of the external morphology in many plant groups. Evolution of the karyotype usually has progressed from symmetry to asymmetry with the evolution of individual chromosomes having evolved from median to terminal forms (Stebbins, 1950).

Dendrobium phalaenopsis, which has the most advanced karyotype on the basis of mean F%, has the advanced features of long internodes, a semi-deciduous habit, and a multiple-flowered inflorescence and the primitive characteristics of herbaceous leaves and an upright growth. Since both advanced and primitive features are exhibited by this species, no definite relationship could be made between the advanced karyotype and external morphological specializations in this species.

The species that possesses one of the most primitive, symmetrical karyotypes, *D. linguella*, is characterized by the advanced features of a pendulous growth, a deciduous habit, long internodes, and a multiple-flowered inflorescence. Again, the external morphology does not reflect the evolution of the karyotype. Within the Eugenanthe section, of which this species is a member, there are varying degrees of pendulous and upright growth exhibited by constituent species, as well as degrees of deciduousness and lengths of the internodes. It is not possible to generalize on a section when such a wide variation in growth habits exists within it. No relationship appears to exist between the evolution of the karyotype on the basis of F% and external morphological specializations in the *Dendrobium* species examined.

Although the sections cannot be distinguished on the basis of chromosome number, chromosome size, S%, or F%, certain characteristics of individual karyotypes make it possible to distinguish some species. As previously mentioned, the chromosome complement of *D. undulatum* can be distinguished by the large pair of heterochromatic subterminal chromosomes accompanied by small median chromosomes. Dendrobium grantii (Figs. 23-24, 80, 104) can easily be distinguished from D. gouldii (Figs. 22, 82, 103) by the absence of the 4 subterminal chromosomes which are found in the latter species. Since no subterminal chromosomes were observed in the Aporum, Callista, Eugenanthe, Latourea, Nigrohirsutae, Pedilonum, Rhopalanthe, or Stachyobium sections, the presence of these chromosomes in an unknown plant cell would eliminate these sections from consideration, if the plant was one of the species used in this study.

The position of the satellite chromosome was inconsistent in all of the species studied. The satellites ranged from being on the second chromosome pair to the eighteenth pair. Dendrobium aggregatum (Figs. 78, 101) consistently showed two pairs of satellite chromosomes, which would indicate that the species is of polyploid origin. The size of the satellites was highly variable among the species. Dendrobium anosmum (Figs. 84, 107) and D. macrophyllum (Figs. 90, 113) had very large and distinctive satellites while those of species in the Ceratobium section were very small and sometimes indistinguishable. The satellites were either heterochromatic, as shown by D. anosmum, or euchromatic, as exemplified by D. phalaenopsis (Figs. 96, 119). The species and sections cannot be separated on the basis of the position, size, or stainability of the satellites.

Karyotype analysis makes it possible to distinguish between two closely related species in the Phalaenanthe section which look very similar in external morphology. Dendrobium biggibum (Figs. 70, 72), a small species with oval flowers and pseudobulbs to 1½ feet tall, has an inflorescence of 4 to 12 flowers about 12 inches long. Dendrobium phalaenopsis (Figs. 71, 73) is similar in habit but much more robust in all parts with the pseudobulbs 4 feet tall or more. The flowers may be 3½ to 4 inches across as compared to a maximum of 2 inches for D. biggibum. For many years taxonomists have considered these to be separate species (Kraenzlin, 1910; Schlechter, 1926). Recently, only D. biggibum has been accepted as a valid species and D. phalaenopsis is considered a botanical variety, D. biggibum var. phalaenopsis (Hawkes, 1965).

The two species have a somatic complement of 38. There is very little difference in mean chromosome length and the difference in mean S% is not significant. The greatest differences in the karyotypes of the two species are found in a comparison of the mean F% and the morphology of the individual chromosomes in each karyotype.

The mean F% of D. biggibum is 42.9 ± 0.6 and that of D. phalaenopsis is 39.7 ± 0.2, showing a significant difference. The two species can be separated on this basis alone, but the most obvious differences are in the morphology of the individual chromosomes. A comparison of the two species on the basis of number of median, submedian, and subterminal chromosomes is:

	D. biggibum	D. phalaenopsis
subterminal	0.0	6.0 ± 0.0
submedian	21.3 ± 2.5	21.7 ± 1.5
median	16.7 ± 2.5	10.3 ± 1.5

The two karyotypes can be separated by the presence of the three pairs of large subterminal chromosomes found in the D. phalaenopsis complement (Fig. 119). These three pairs of chromosomes are the largest found in the karyotype of this species. Since D. phalaenopsis has an increase in three pairs of subterminal chromosomes at the loss of three pairs of median chromosomes as compared to D. biggibum, it would appear that this is a simple case of unequal translocation, disregarding the possibility of convergent evolution. This assumption is possible if the three largest chromosome pairs in D. biggibum are median. Unfortunately, three of the largest five pairs of chromosomes of D. biggibum are submedian. This does not disprove the possibility of an unequal translocation. It just shows that many further translocations have occurred in the D. biggibum karyotype since it was modified to that of D. biggibum var. phalaenopsis. Even though the superficial appearance of the chromosomes may have been altered by unequal reciprocal translocations of chromosal segments, such changes appear to have had little effect on the external morphology of the plant. A competent taxonomist might re-examine these two species to see if any morphological characters can be found to indicate that they are really separate species rather than varieties.

Although it has been shown that the sections, as classified by Schlechter (1912), cannot be distinguished by karyotype analysis, a few individual species can be recognized by the combination of chromosome size, S%, and F%. Little relationship was found among specializations in the karyotype on the sectional level and the external morphology of the plant although a few species showed what appeared to be a weak relationship.

Genome Relationships

Meiosis in four intrasectional diploid hybrids of Ceratobium was analyzed (Table VIII; Figs. 122-128). Twenty-five pollen mother cells

Table VIII. Mean chromosome configurations at metaphase I of meiosis of within-section hybrids of Ceratobium, 2n=38.

Hybrid	Mean Configuration Per PMC	Number of PMCs* Observed
mirbellianum x johannis, #1	19.0 II	25
#2	19.0 II	25
d'albertsii x mirbellianum, #1	19.0 II	25
#2	19.0 II	25
#3	19.0 II	25
strebloceras x d'albertsii, #1	19.0 II	25
#2	19.0 II	25
#3	19.0 II	25
strebloceras x undulatum, #1	19.0 II	25
#2	19.0 II	25
#3	19.0 II	25

*Pollen mother cells.

Table IX. Mean chromosome configurations at metaphase I of meiosis of between-section hybrids of Phalaenanthe and Ceratobium, 2n=38.

Hybrid	Mean Configuration Per PMC	Number of PMCs Observed
phalaenopsis x gouldii	17.08II + 3.84I	25
phalaenopsis x grantii	16.60II + 4.80I	25
dicuphum x gouldii, #1	17.20II + 3.60I	25
#2	16.09II + 5.83I	23
biggibum x d'albertsii, #1	16.72II + 4.56I	25
#2	16.38II + 5.25I	24
#3	17.43II + 3.13I	23
phalaenopsis x d'albertsii, #1	17.16II + 3.68I	25
#2	17.21II + 3.57I	24
#3	16.14II + 5.73I	22

Table X. Mean chromosome configurations at Metaphase I of meiosis of a between-section hybrid of Phalaenanthe and Latourea, 2n=38.

Hybrid	Mean Configuration Per PMC	Number of PMCs Observed
johnsoniae x phalaenopsis	2.06II + 33.88I	16

(PMCs) at Metaphase I of each plant were examined and meiosis showed consistently 19 bivalent chromosomes (Figs. 139-142). Two siblings of D. mirbellianum x johannis were studied and three siblings of each of the remaining three primary hybrids, D. d'albertsii x D. mirbellianum, D. strebloceras x D. d'albertsii, and D. strebloceras x D. undulatum, were investigated.

The bivalent chromosomes were either rod or ring shape with terminal chiasmata and the size of the bivalents differed within each complement. Some of the bivalents were conspicuously large and heteropycnotic and were readily visible at late prophase and metaphase of meiosis. Metaphase I configurations of D. strebloceras x undulatum were characterized by the presence of conspicuously large, dark-staining bivalents (Fig. 140). The somatic chromosome complement of D. undulatum (Figs. 81, 105) contains one very large pair of subterminal, heterochromatic chromosomes and that of D. strebloceras contains a slightly smaller subterminal chromosome pair. The large heterochromatic chromosomes in the somatic complement of the parental species appear to correspond to the large bivalents observed in Metaphase I of the primary hybrid.

One hundred cells were analyzed in microspore division of each plant of the intrasectional Ceratobium hybrids. The products of meiosis were normal tetrads with 19 chromosomes distributed to each microspore (Table XI; Figs. 150-151). No dyads or microcytes (mcs) were observed in pollen mitosis of any of the within-section Ceratobium hybrids.

The five diploid intersectional hybrids involving Phalaenanthe and Ceratobium (Figs. 131-138) exhibited similarly irregular meiotic

Table XI. Sporad formation in <u>Dendrobium</u> primary hybrids.

Species and Hybrids	Sporad					Total
	Tetrad	Tetrad + mcs*	Dyad	Dyad + mcs	Monad	
Ceratobium x Ceratobium						
mirbellianum x johannis, #1	100					100
#2	100					100
d'albertsii x mirbellianum, #1	100					100
#2	100					100
#3	100					100
strebloceras x d'albertsii, #1	100					100
#2	100					100
#3	100					100
strebloceras x undulatum, #1	100					100
#2	100					100
#3	100					100
Phalaenanthe x Ceratobium						
phalaenopsis x gouldii	93	3	4			100
phalaenopsis x grantii	89	2	9			100
dicuphum x gouldii, #1	97		3			100
#2	92	4	3	1		100
biggibum x d'albertsii, #1	95	2	3			100
#2	93	5	2			100
#3	97	2	1			100
phalaenopsis x d'albertsii, #1	95	1	4			100
#2	94	3	3			100
#3	87	4	7	2		100
Phalaenanthe x Latourea						
phalaenopsis x johnsoniae	22	9	147	5	17	200

*Microcytes.

Plate 14. Vegetative and floral morphology of primary hybrids of *Dendrobium* species.

Figure:

122. D. strebloceras x d'albertsii (0.7X).

123. D. strebloceras x d'albertsii (0.1X).

124. D. strebloceras x undulatum (0.7X).

125. D. d'albertsii x mirbellianum (0.7X).

126. D. d'albertsii x mirbellianum (0.1X).

127. D. mirbellianum x johannis (1.0X).

128. D. mirbellianum x johannis (.15X).

129. D. johnsoniae x phalaenopsis (.15X).

130. D. johnsoniae x phalaenopsis (0.7X).


127
128
129
130

behavior (Table IX). Between 22 and 25 pollen mother cells were studied at Metaphase I of each plant and the bivalents varied in number from 14 to 19 and the univalents from 0 to 10 (Figs. 143-147). Most of the PMCs formed 16 to 18 bivalents and from 2 to 6 univalents. One plant each of D. phalaenopsis x D. gouldii and D. phalaenopsis x D. grantii, 2 siblings of D. dicuphum x D. gouldii, and 3 siblings of each of the remaining two intersectional hybrids, D. phalaenopsis x D. d'albertsii and D. biggibum x D. d'albertsii, were analyzed.

Dendrobium phalaenopsis x D. gouldii (Fig. 138) formed from 14 to 19 bivalents and from 0 to 10 univalents with a mean of 17.08 and 3.84, respectively (Table IX; Fig. 143). Two or more heteromorphic bivalents were visible in many of the metaphase figures with a large range in size of the univalents. In many of the cells, the two or more large heterochromatic bivalents observed may be the equivalent of the three large heterochromatic chromosome pairs found in the somatic complement of D. phalaenopsis (Figs. 96, 119). The products of meiosis were predominately tetrads, 93%, with a few tetrads with microcytes and dyads. The production of tetrads reflects the relatively high degree of chromosome pairing at meiosis.

Dendrobium phalaenopsis x D. grantii (Fig. 137) formed from 14 to 18 bivalents and from 2 to 10 univalents with an average of 16.60 and 4.80, respectively (Fig. 147). Unlike the previous hybrid, few large heterochromatic bivalents were observed in the metaphase figures. The somatic chromosomes of D. grantii (Fig. 104) differ from those of D. gouldii (Fig. 103) by the conspicuous absence of the large sub-terminal chromosomes seen in the other members of the Ceratobium section. The absence of these heterochromatic chromosomes in the

Plate 15. Vegetative and floral morphology of primary hybrids of Dendrobium species.

Figure:

131. D. biggibum x d'albertsii (0.1X).

132. D. biggibum x d'albertsii (0.7X).

133. D. phalaenopsis x d'albertsii (.15X).

134. D. phalaenopsis x d'albertsii (0.6X).

135. D. dicuphum x gouldii (0.1X).

136. D. dicuphum x gouldii (0.9X).

137. D. phalaenopsis x gouldii (0.7X).

138. D. phalaenopsis x grantii (0.7X).

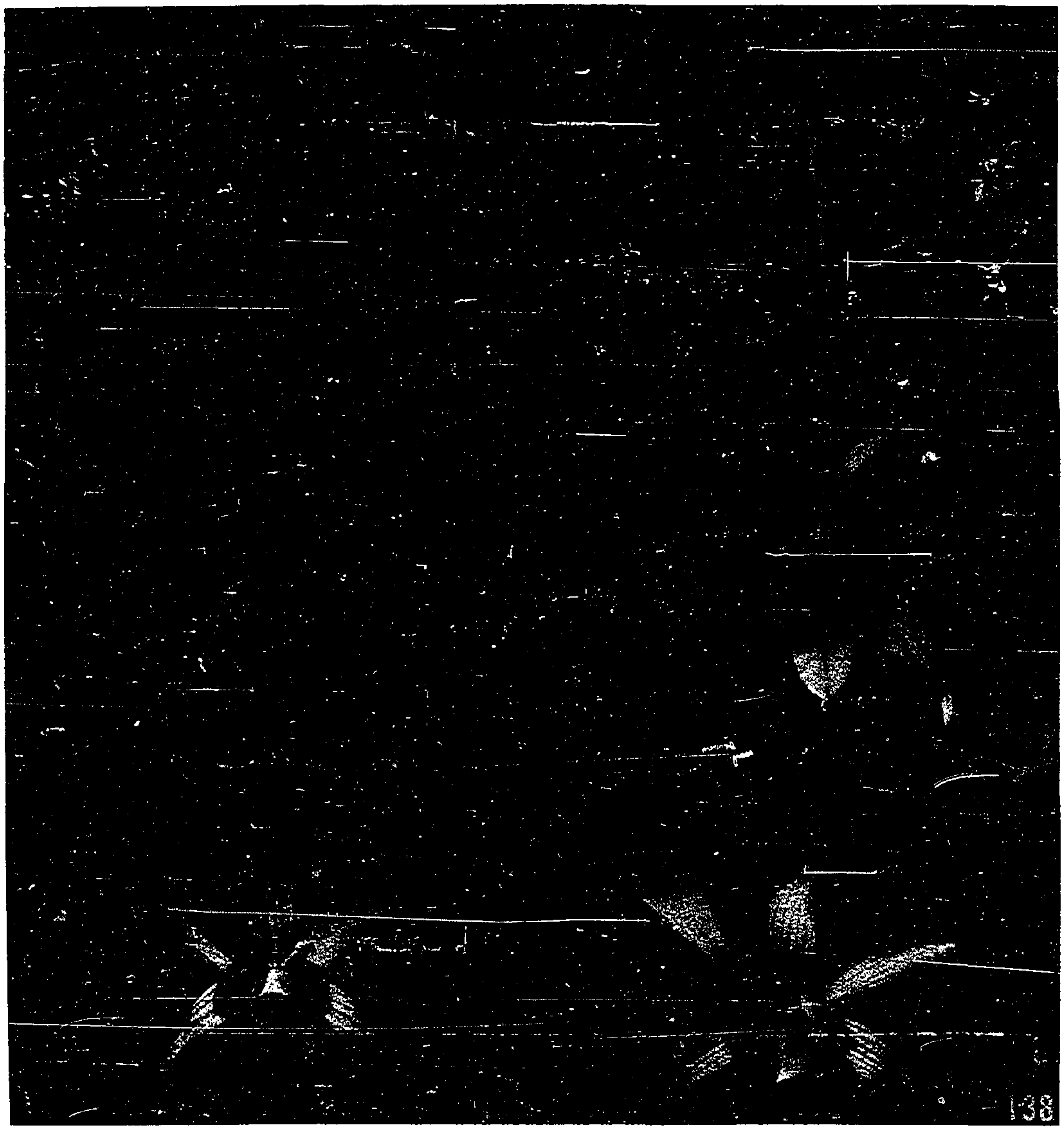
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Plate 16. Metaphase I configurations of primary hybrids of <u>Dendrobium</u> species (3300X).

Figure:

139. D. strebloceras x d'albertsii, 19II.

140. D. strebloceras x undulatum, 19II.

141. D. d'albertsii x mirbellianum, 19II.

142. D. mirbellianum x johannis, 19II.

143. D. phalaenopsis x gouldii, 15II + 8I.

144. D. dicuphum x gouldii, 17II + 4I.

145. D. phalaenopsis x d'albertsii, 18II + 2I.

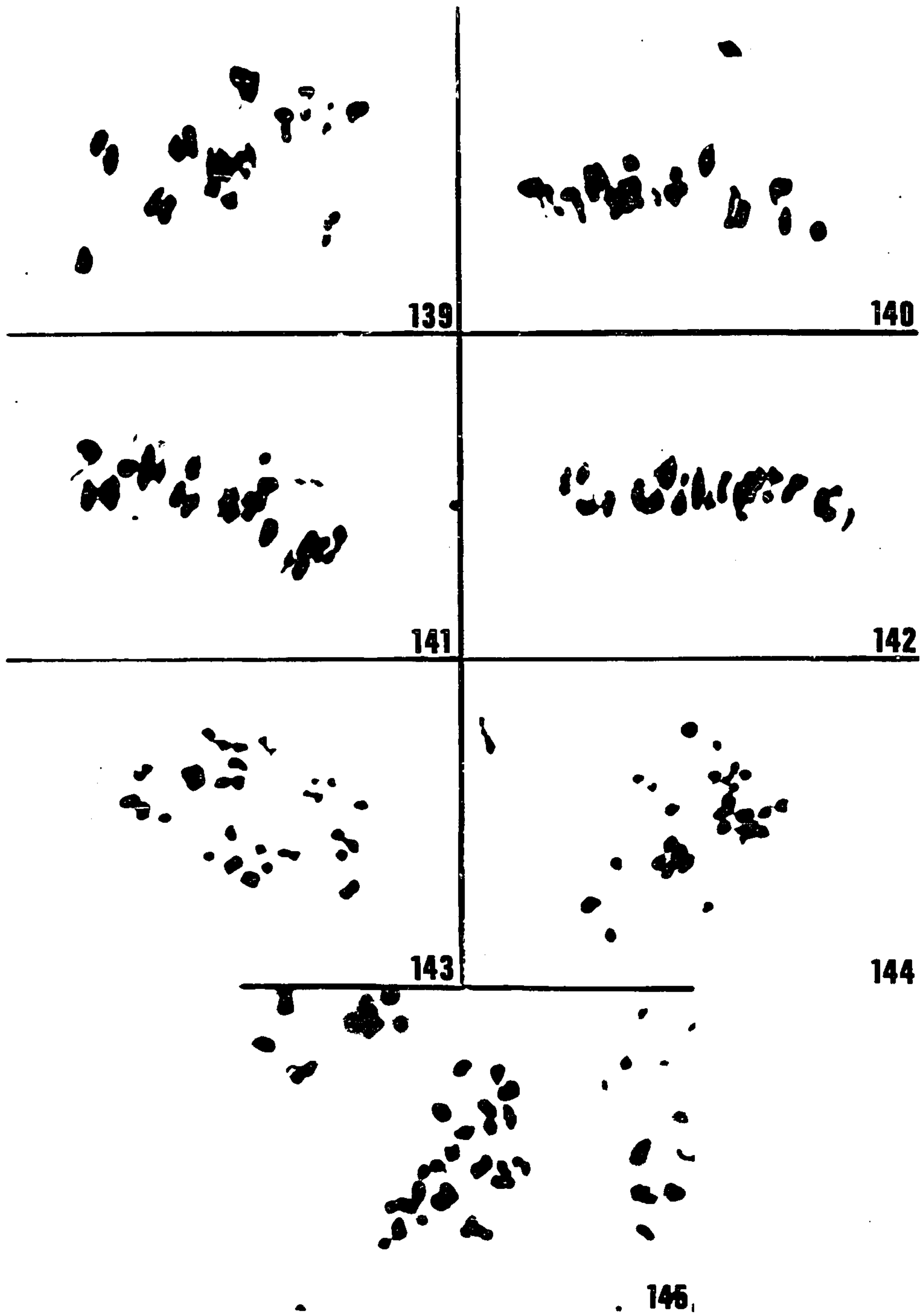
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Plate 17A. Metaphase I configurations of primary hybrids of <u>Dendrobium</u> species (3300X).

Figure:

146. D. biggibum x d'albertsii, 18II + 2I.

147. D. phalaenopsis x grantii, 17II + 4I.

Plate 17B. Microspore division in primary hybrids of <u>Dendrobium</u> species.

Figure:

148. D. johnsoniae x phalaenopsis (1800X).

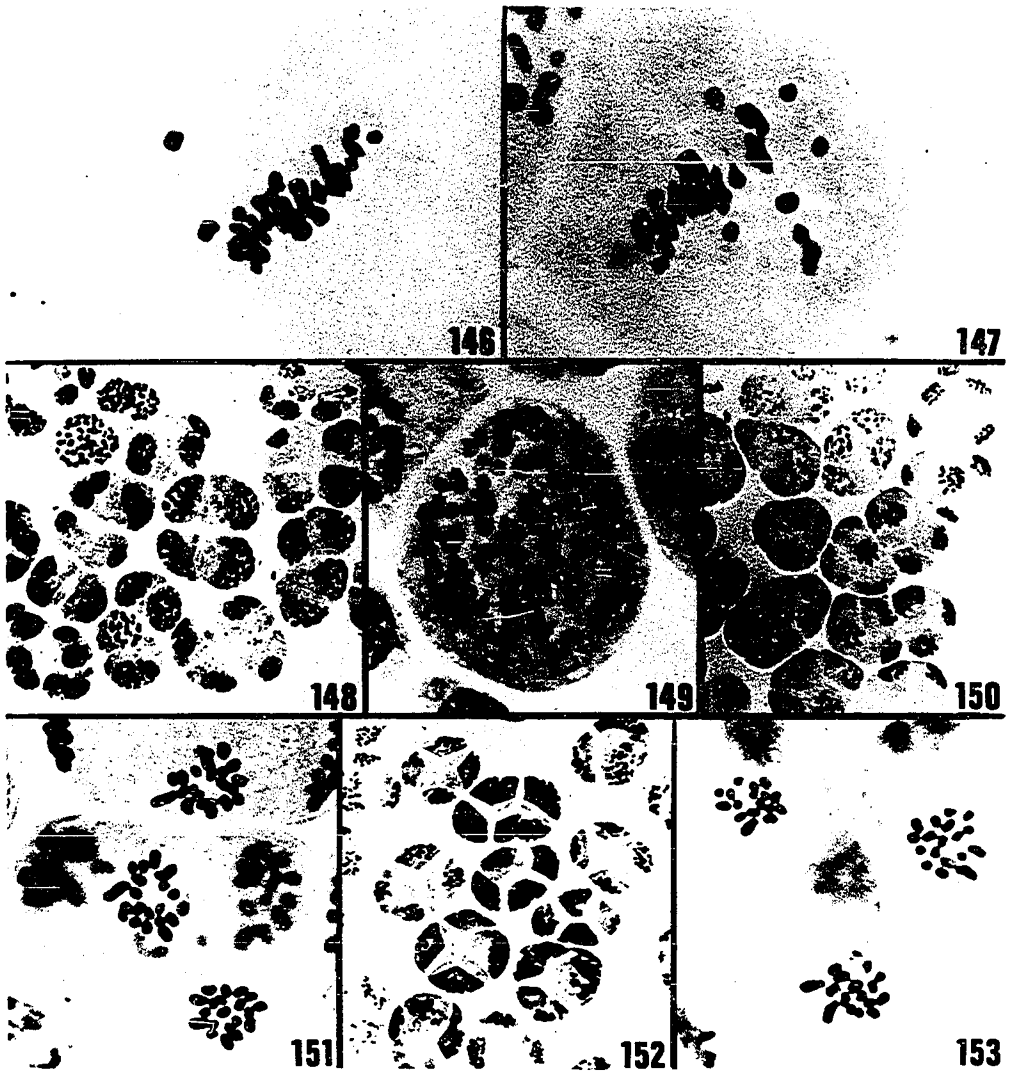
149. D. johnsoniae x phalaenopsis (3300X).

150. D. strebloceras x d'albertsii (1800X).

151. D. strebloceras x d'albertsii (3300X).

152. D. phalaenopsis x d'albertsii (1800X).

153. D. phalaenopsis x d'albertsii (3300X).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somatic complement may be related to the general lack of dark-staining bivalents in the primary hybrid. Pollen mitosis showed mainly tetrads, 89%. Of all the Phalaenanthe x Ceratobium hybrids studied, this one plant exhibited the highest percentage of dyads, 9%.

The average number of bivalents in the two plants of D. dicuphum x D. gouldii (Figs. 135-136) varied from 16.09 to 17.20 with a mean of 16.64 (Fig. 144). The average number of univalents ranged from 3.60 to 5.83 with a mean of 4.72. One of the siblings, #2, produced the lowest average number of bivalents found in the Phalaenanthe x Ceratobium hybrids. Very few heterochromatic bivalents were observed although some heteromorphic bivalents with precocious separations were seen in a few of the metaphase configurations. This precocious separation indicates a weak synaptic force in the heteromorphic bivalents. Microspore division showed a predominance of tetrads, from 92 to 97%, with relatively few tetrads with microcytes, dyads, and dyads with microcytes.

The three siblings of D. biggibum x D. d'albertsii (Figs. 131-132) exhibited a variation in average number of bivalents from 16.38 to 17.43 and of univalents from 3.13 to 5.25 (Fig. 146). The means of the bivalents and univalents of the three plants are 16.84 and 4.31, respectively. Two or more heterochromatic bivalents were observed in many of the metaphase figures. The products of meiosis were mostly tetrads, from 93 to 97%, with few dyads and tetrads with microcytes.

The plants examined of D. phalaenopsis x D. d'albertsii (Figs. 133-134) showed a variation in average number of bivalents from 16.14 to 17.21 with a mean of 16.83 (Fig. 145). The average number of univalents ranged from 3.57 to 5.73 with a mean of 4.33. Between two and three dark-staining bivalents were observed at Metaphase I and these were also evident in prophase of meiosis. Microspore division showed between 87 and 95% tetrads, with a few tetrads with microcytes, dyads, and dyads with microcytes also visible (Fig. 152). The number of chromosomes in each microspore varied from 17 to 21 with an average of approximately 19 (Fig. 153).

The irregular meiosis in the diploid intersectional hybrid of Phalaenanthe and Latourea, D. phalaenopsis x D. johnsoniae (Figs. 129-130), revealed variations in number of bivalents from 6 to 0 with a mean of 2.06 and of univalents from 26 to 38 with a mean of 33.88 (Table X). No definite metaphase plates were formed during meiosis. The univalents were of variable size and scattered throughout the cell or were in masses. Many of the univalents were sticky and not well differentiated from the cytoplasm. The movement of chromosomes to either pole at Anaphase I was not orderly enough to produce the normal daughter nuclei, with restitution of the nucleus common for the majority of the pollen mother cells. The products of meiosis were mainly dyads. Tetrads, monads, and tetrads and dyads with microcytes were also observed (Table XI; Figs. 148-149).

The results of the present study agree with the data previously reported on genome relationships in Dendrobium hybrids. Results presented here as well as those of Kamemoto, Shindo, and Kosaki (1964) in Ceratobium section hybrids showed 19 bivalents and the products of meiosis were normal tetrads with 19 chromosomes distributed to each microspore. The five intersectional Phalaenanthe x Ceratobium hybrids analyzed varied in number of bivalents from 16.09 to 17.43. The seven hybrids of the same two sections studied by Kamemoto, Shindo, and

Kosaki had a range of 15.76 to 18.92 bivalents. The three Phalaenanthe x Ceratobium hybrids investigated by Dorn and Kamemoto (1962) showed a range of 15.3 to 17.9 bivalents. In the one intersectional Phalaenanthe x Latourea hybrid analyzed in the present study, the average number of bivalents was 2.06. A similar intersectional hybrid analyzed by Kamemoto, Shindo, and Kosaki (1964) revealed an average of 1.81 bivalents. No significant differences are seen in the results of this research and that of previous workers on genome relationships in hybrids involving the Ceratobium, Latourea, and Phalaenanthe sections.

With the results of the present research and that of previous researchers (Dorn and Kamemoto, 1962; Kamemoto, Shindo, and Kosaki, 1964), meiosis of 26 Dendrobium primary hybrids has been analyzed. Twelve hybrids within the Ceratobium section showed consistently 19 bivalents. Eleven hybrids between the Ceratobium and Phalaenanthe sections exhibited an average, with standard deviation, of 17.14 ± 0.87 bivalents, 3.69 ± 1.75 univalents, and 0.01 ± 0.02 trivalents. In the two intersectional Phalaenanthe and Latourea hybrids examined, 1.94 ± 0.18 bivalents, 34.04 ± 0.32 univalents, and 0.16 ± 0.23 trivalents were observed. Only one hybrid of Ceratobium and Latourea has been analyzed with 10.83 bivalents and 16.31 univalents were reported.

Analyses of all these hybrids indicate that the genomes of the Ceratobium and Phalaenanthe sections are closely homologous and those of the Latourea are more distantly related. The three hybrids studied which involved the Latourea section indicate that this section's genomes are more closely related to those of the Ceratobium section than to those of the Phalaenanthe section. The separation of the parental species of the hybrids examined into the three groups, Ceratobium, Phalaenanthe, and Latourea, appears to be valid on the basis of external morphology and genome relationships. If evolution of these three groups occurred in a sequential manner, divergence might have proceeded from Latourea to Ceratobium to Phalaenanthe, on the basis of genome relationships. Since no significant differences were observed among sections in S% and F%, no support for this theory can be made from the karyotype analyses.

A classification scheme was earlier proposed showing relationships between sections based on the results of the compatibility studies. In those studies it was observed that the Latourea section is more closely related to the Phalaenanthe than the Ceratobium group. The genome studies disprove that idea, and so a new scheme based on sexual compatibility studies, karyotype analyses of the species, and genome relationships is:

Closer to Ceratobium	Equal or Undetermined	Closer to Phalaenanthe
Latourea	Aporum	Eugenanthe
Pedilonum	Callista	Nigrohirsutae
Stachyobium	Rhopalanthe	

Although it was not possible to separate the classical taxonomic sections of Dendrobium on the basis of chromosome number, chromosome size, S%, and F%, certain species can be characterized and distinguished from the remaining species by these features. The genome relationships indicate that the Ceratobium, Latourea, and Phalaenanthe sections are valid groups.

SUMMARY

Sexual compatibility, karyotype analysis, and genome relationship studies were made with species in the genus Dendrobium of the family Orchidaceae.

A hybridization study was made utilizing 38 species of 10 sections in 44 combinations. A total of 783 pollinations were made with 164 fruits harvested, of which 113 produced viable crosses. Five intra-sectional and 20 intersectional combinations resulted in viable seedlings. Phalaenanthe x Phalaenanthe exhibited the highest percentage of fruits and successful crosses while Callista x Eugenanthe had the lowest. The Eugenanthe x Eugenanthe combination showed little compatibility among the species within the section and equal or more compatibility with the Ceratobium, Phalaenanthe, and Pedilonum sections. The discrepancy between the number of registered hybrids in this combination and the hybridization study results may be explained by the large number of species in the Eugenanthe section and the length of time they have been in cultivation. The percentage of non-aborted embryos was determined under microscopic examination of each fruit harvested. The separation of all the species into Schlechter's sections was not possible on the basis of their crossability or percentage of non-aborted embryos.

The chromosome numbers of 33 species in 11 sections were determined, of which 31 were 2n=38 and 2 were 2n=40. The chromosome complements of five of these species had not previously been reported. No attempt was made to correlate somatic number of the species with the sections, since six of the sections studied contain species of both 2n=38 and

2n=40, as reported in the literature.

Detailed examinations of chromosome morphology were made of 23 species in 11 sections. The mean chromosome size was as variable among species within the sections as between the sections. The sections could not be distinguished by the average chromosome length of their constituents. No relationship was found between chromosome size and geographical and climatological distribution in the 23 species studied.

The mean S% of each species and the average of each section was calculated. Individual sections could not be distinguished on the basis of S% although some individual species could be detected by S% in conjunction with other morphological characteristics of the karyotypes. An attempt was made to show a relationship between specializations in the karyotype and specializations in external morphological characteristics of the species. The evolution of the karyotypes was not reflected in the external morphological specializations of the sections although a few species did show what appeared to be a valid relationship, on the basis of mean S%.

The mean F% was determined for all of the species studied. Although a significant difference in mean F% was shown to exist among species in different sections, just as much variation was shown among species in the same section. An attempt was made to correlate mean F% of the species and sections with vegetative morphological specializations. No relationship appeared to exist between the evolution of the karyotype on the basis of F% and external morphological specializations in the species examined.

Although the sections could not be distinguished on the basis of chromosome number, chromosome size, S%, or F%, certain characteristics of individual karyotypes made it possible to distinguish a few species from all the rest. Dendrobium undulatum was characterized by large heterochromatic subterminal chromosomes. Two closely related species, D. phalaenopsis and D. biggibum, were separable by the presence of six subterminal chromosomes in the former species and their absence in the latter.

Meiosis in four intrasectional Ceratobium hybrids showed consistently 19 bivalents and the products of meiosis were normal tetrads with 19 chromosomes distributed to each microspore. Heterochromatic bivalents were observed in some of the metaphase configurations. Five intersectional Ceratobium x Phalaenanthe hybrids displayed an average of 16.80 bivalents and 4.40 univalents. Microspore division exhibited an average of 93.2% tetrads and 3.9% dyads, with tetrads and dyads with microcytes also observed. Meiosis in a Phalaenanthe x Latourea hybrid showed 2.06 bivalents and 33.88 univalents with the products of meiosis being tetrads, dyads, and tetrads and dyads with microcytes. Heterochromatic and heteromorphic bivalents were observed in the intersectional hybrids. The results indicate that the genomes within the Ceratobium section are closely homologous; the genomes of Ceratobium and Phalaenanthe are closely related; and the genomes of Latourea are more closely related to Ceratobium than to Phalaenanthe.

A classification scheme was shown exhibiting the relationship of the sections studied as related to the Ceratobium and Phalaenanthe sections. Although the sections could not be distinguished by sexual compatibility or karyotype analysis, certain species could be distinguished by these measurements. Genome relationships indicated that the Ceratobium, Phalaenanthe, and Latourea sections are valid groups.

APPENDIX

Appendix A. Primary Dendrobium hybrids registered through 1967.

Hybrid	Parentage	Year Registered
Adrasta	pierardii x superbum (anosmum)	1892
Aeneas	crystallinum x moniliforme (monile)	1893
Ainsworthii	aureum (heterocarpum) x nobile	1874
Aitkenvale	compactum (phal.) x williamsianum	1965
Albanense	superbiens x undulatum	1948
Albertine	biggibum x d'Albertsii	
Alex MacKenzie	grantii x affine	1961
Alice Noda	undulatum x schulleri	1954
Alice Spalding	tokai x undulatum	1950
Andrew Persson	speciosum x falcorostrum	1960
Aoyama	aduncum x moniliforme (monile)	1924
Arcuatum	schroderianum (phal.) x violaceoflavens	
Arno	tokai x schulleri	1954
Aropa	johnsoniae x forbesii	1965
Arthur Ashworth	brymerianum x dalhousieanum (pulchellum)	1906
Astraea	crassinode x luteolum	1895
Atro-Brymerianum	atroviolaceum x brymerianum	1909
Audrey Chinn	grantii x johannis	1958
Australia	biggibum x toftii	
Backhousei	nobile x thyrsiflorum	1896
Bangkhen	stratiotes x schulleri	1950
Bangkok	phalaenopsis x taurinum	
Barbara Gittens	moschatum x clavatum	1953
Barbara Moore	affine x gouldii	1962
Barbatulo-Chlorops	barbatulum x chlorops	
Bardo Rose	falcorostrum x kingianum	1961
Benita	aureum (heterocarpum) x falconeri	1893
Bluebird	goldiei (superbiens) x tokai	1950
Blue Gloucester	superbiens x toftii	1966
Boissyense	biggibum x schroderianum (phal.)	1926
Bougainville	johnsoniae x phalaenopsis	1961
Brisbane	superbiens x veratrifolium	1940
Bryan	luteolum x wardianum	1893
Caesar	schroderianum (phal.) x stratiotes	
Calvin Morioka	goldiei (superbiens) x veratrifolium	1953
Caprice	macrophyllum x undulatum	1939
Cascade	affine x phalaenopsis	1964
Cassiope	moniliforme (monile) x nobile	1890
Champagne	undulatum x mirbellianum	1951
Charm Devi	schulleri x violaceoflavens	1952
Cheltenhamense	aureum (heterocarpum) x luteolum	1893
Chieno	undulatum x dicuphum	1964
Chlorostele	linawianum x wardianum	1887
Clara Cooper	schroderianum (phal.) x strebloceras	1945

Appendix A. (Continued) Primary Dendrobium hybrids registered through 1967.

Hybrid	Parentage	Year Registered
Clarense	findlayanum x signatum	1903
Colin Potter	phalaenopsis x toftii	1944
Constance	undulatum x lasianthera	1940
Corella	aureicolor x phalaenopsis	1961
Corningianum	lituiflorum x nobile	1876
Crassinode-Wardianum	crassinode x wardianum	
Crepidato-Nobile	crepidatum x nobile	1899
Cybele	findlayanum x nobile	1887
Cypheri	crassinode x findlayanum	1902
Dalhou-Nobile	dalhousieanum (pulchellum) x nobile	1900
Dalvey	bifalce x phalaenopsis	1951
Dana	aries x veratrifolium	1950
Dang Toi	goldiei (superbiens) x undulatum	1941
David Baver	johannis x phal. var. compactum	1956
David Sander	schroderianum (phal.) x toftii	1944
Desaputra	veratrifolium x dalhousieanum (pulchellum)	1963
Devesianum	stratiotes x strebloceras	
Dominianum	linawianum x nobile	1864
Dulce	linawianum x aureum (heterocarpum)	1892
Edinense	crassinode x regium	1925
Ellen	kingianum x tetragonum	1928
Elsie Cox	goldiei (superbiens) x delicatum	1961
Emily Brant	superbum (anosmum) x dearei	1955
Emmy	aemulum x kingianum	1967
Endocharis	aureum (heterocarpum) x moniliforme (monile)	1876
E. P. Boyle	stratiotes x phalaenopsis	1954
Erma Jean	grantii x schulleri	1952
Farmeri-Thyrsiflorum	farmeri x thyrsiflorum	
Findlayano-Wardianum	findlayanum x wardianum	1896
Florence	bensoniae x nobile	1903
Formidible	formosum x infundibulum	1967
Formoso-Lowii	formosum x lowii	1898
442nd Infantry	taurinum x veratrifolium	1946
Francesco Allavena	crystallinum x superbum (anosmum)	1938
Franklin W. Gamble	formosum x dalhousieanum (pulchellum)	1957
Frederick G. Krauss	grantii x lasianthera	1950
Gemma	aureum (heterocarpum) x superbum (anosmum)	1895
Geo MacKenzie	strebloceras x affine	1961

Appendix A. (Continued) Primary Dendrobium hybrids registered through 1967.

Hybrid	Parentage	Year Registered
Gillian Leaney	delicatum x kingianum	1965
Gloucester Charm	veratrifolium x canaliculatum	1966
Gloucester Crimson	aries x phalaenopsis	1966
Gloucester Dawn	mirbellianum x canaliculatum	1966
Gloucester Sands	undulatum x canaliculatum	1963
Golden Mac	macrophyllum x schulleri	1966
Gracia Lewis	macrophyllum x superbiens	1950
Gregor Duruty	phalaenopsis x goldiei (superbiens)	1957
Hanburyi	dalhousieanum (pulchellum) x fimbriatum	1918
Harold	findlayanum x linawianum	1896
Hawaii	phalaenopsis x tokai	1938
Hawaiian Sunshine	undulatum x aggregatum	1965
Helen Park	biggibum x veratrifolium	
Hunteri	brymerianum x nobile	1902
Ida Ann	phalaenopsis x capra	1959
Illustre	chrysotoxum x dalhousieanum (pulchellum)	1895
Infunderae	infundibulum x sanderae	1946
Isabel Sander	dearei x sanderae	1937
Isis	hercoglossum (linguella) x moniliforme (monile)	1901
Jane Leaney	delicatum x speciosum	1965
Jane Warne	dearei x schutzei	1944
Janice Tanaka	aries x taurinum	1949
Jaquelyn Thomas	gouldii x phalaenopsis	1949
Jean Sutton	tokai x schroderianum (phal.)	1958
Jessie Pung	taurinum x schulleri	1955
Joanne Sawers	tokai x veratrifolium	1951
John Laycock	pulchrum x schroderianum (phal.)	
John Nauen	formosum x ovipositoriferum	1949
Judy Leroy	canaliculatum x dicuphum	1961
Juweeltje	biggibum x strebloceras	
Kaimuki	johannis x senile	1950
Kaipu	mirbellianum x johannis	1958
Kakela	gouldii x undulatum	1946
Kapalama	gouldii x superbiens	1952
Karen Okamoto	toftii x gouldii	1956
Kauai	superbiens x taurinum	1947
Kenneth	bensoniae x maccarthiae	1896
Kila Blue	toftii x williamsianum	1967
Klong Rai	undulatum x dalhousieanum (pulchellum)	1956
Kokoda Trail	stratiotes x johnsoniae	1963
Kona	lasianthera x macrophyllum	1942
Kukui	moschatum x phalaenopsis	1945

Appendix A. (Continued) Primary Dendrobium hybrids registered through 1967.

Hybrid	Parentage	Year Registered
Leah Dietz	grantii x gouldii	1951
Leahi	biggibum x taurinum	1945
Leeanum	phalaenopsis x superbiens	
Lily Doo	macrophyllum x phalaenopsis	1950
Lim Tar Fang	schulleri x phalaenopsis	1952
Lisa Ann	stratiotes x toftii	1958
Lotus	nobile x suavissimum (chrysotoxum)	1901
Louisae	schroderianum (phal.) x veratrifolium	1935
Louis Bleriot	schroderianum (phal.) x superbiens	
Lowana Nioka	canaliculatum x d'albertsii	1962
Lum Goo	gouldii x stratiotes	1949
Mac-jap	maccarthiae x moniliforme (monile)	1904
Mantinii	fimbriatum var. oculatum x nobile	1901
Marguerite K. Ashford	macrophyllum x stratiotes	1955
Marietta Chang	aries x undulatum	1950
Mary Kong	strebloceras x schulleri	1962
Maureen Jansen	odoardii x undulatum	1965
Medusa	violaceoflavens x undulatum	1949
Mem. Edward Trevor	ostrinoglossum x phalaenopsis	1962
Mem. Gordon Hew	schulleri x gouldii	1951
Mentor	primulinum x superbum (anosmum)	1893
Micans	lituiflorum x wardianum	1879
Milne Bay	stratiotes x williamsianum	1966
Moira Stewart	gouldii x mirbellianum	1960
Morgenster	stratiotes x violaceoflavens	1940
Moses Mark	d'albertsii x mirbellianum	1961
Mount Waialeale	d'albertsii x veratrifolium	1947
Mousmee	bronckartii x thyrsiflorum	1941
Mrs. Alfred Rogers	findlayanum x hildebrandii	1907
Murrayi	albosanguineum x nobile	1895
Murrhiniacum	nobile x wardianum	1888
Myra	linawianum x signatum	1904
Nellie Slade	atroviolaceum x forbesii	1965
Nelly Slander	dearei x formosum	1934
Neo Hawaii	grantii x phalaenopsis	1944
Neoh Teik-Hong	strebloceras x grantii	1964
Nestor	parishii x superbum (anosmum)	1893
New Guinea	macrophyllum x atroviolaceum	1956
Ngadiman	trilamellatum x schulleri	1966
Niobe	nobile x tortile	1893
Oahu	grantii x taurinum	1949
Obscurum	chrysotoxum x thyrsiflorum	
Olive	schulleri x mirbellianum	1958

Appendix A. (Continued) Primary Dendrobium hybrids registered through 1967.

Hybrid	Parentage	Year Registered
Ong Siew Hong	fleischeri x stratiotes	1956
Ophir	aureum (heterocarpum) x signatum	1902
Orchidwood	biggibum x phalaenopsis	1934
Orgon	flaviflorum x moschatum	1934
Pauline	phalaenopsis x undulatum	1932
Pax	fleischeri x schroderianum (phal.)	1938
Peter Peterson	undulatum x toftii	1956
Phyllis	violaceoflavens x superbiens	1949
Porphyrogastrum	dalhousieanum (pulchellum) x superbum (anosmum)	1888
Princess Stephanie	mirbellianum x biggibum	1962
Puhala	gouldii x mirbellianum	1952
Punaluu	aries x superbiens	1948
Püppchen	schroderianum (phal.) x undulatum	
Queensland	stratiotes x superbiens	1940
Radians	lowii x sculptum	
Red Wings	d'albertsii x johannis	1954
Rhodopterygium	parishii x pierardii	
Rhodostoma	superbum (anosmum) x sanguinolentum	1870
Rickie Cornetti	veratrifolium x toftii	1955
Roeblingianum	nobile x ruckeri	1893
Roger Sander	mirbellianum x schroderianum (phal.)	1936
Rolfeae	nobile x primulinum	
Rosalind Choon Lin	undulatum x trilamellatum	
Rose Marie	leporinum x phalaenopsis	1937
Rosy Tips	canaliculatum x phalaenopsis	1960
Royal Princess	aureum (heterocarpum) x regium	1912
Rudolf Lieske	lasianthera x superbiens	1953
Ruth Thomas	schroderianum (phal.) x schulleri	1950
Salak	stratiotes x undulatum	
Samarai	stratiotes x antennatum	1967
Sander's Crimson	schroderianum (phal.) x taurinum	1935
Sarie Marijs	d'albertsii x schroderianum (phal.)	
Saro Roig	tokai x gouldii	1966
Saskia	superbiens x biggibum	1951
Schneiderianum	aureum (heterocarpum) x findlayanum	1887
Sea Bird	schutzei x formosum	1953
Shan Leaney	gracillimum x gracilicaule	1965
Shibata	taurinum x tokai	1947
Snow White	nobile x sanderae	1949
Specio-Kingianum	kingianum x speciosum	1892
Statterianum	bensoniae x crystallinum	
Stratius	moniliforme (monile) x dalhousieanum (pulchellum)	1892

Appendix A. (Continued) Primary Dendrobium hybrids registered through 1967.

Hybrid	Parentage	Year Registered
Strattokai	stratiotes x tokai	1947
Sunda Islands	stratiotes x veratrifolum	1949
Suzanne	phalaenopsis x tetragonum	1965
Sybil	crassinode x linawianum	1893
Sylvia Morley	johannis x stratiotes	1958
Tan Chye Siam	veratrifolium x lasianthera	1949
Tan Ghim Kheng	goldiei (superbiens) x gouldii	1958
Taurus	taurinum x undulatum	1941
Thistledown	infundibulum x dearei	1957
Thomas Warne	sanderae x schutzei	1948
Three Star	johannis x goldiei (superbiens)	1954
Tocuphum	dicuphum x tokai	1951
Tom Vong Hagt	demmenii x schroderianum (phal.)	
Triumph	dalhousieanum (pulchellum) x thrysiflorum	1914
T. Shioi	gouldii x taurinum	1951
Tusco	toftii x johannis	1957
Ursula	undulatum x veratrifolium	
Vannerianum	falconeri x moniliforme (monile)	1887
Variabilis	nobile x thwaitesiae	1921
Varsity	stratiotes x taurinum	1948
Veitchii	moniliforme (monile) x wardianum	1890
Venus	falconeri x nobile	1890
Vera Bong	schulleri x veratrifolium	1965
Verigrant	veratrifolium x grantii	1951
Verninha	undulatum x d'albertsii	1961
Veruna	phalaenopsis x veratrifolium	1954
Virginia	bensoniae x moniliforme (monile)	1890
Walter Carter	stratiotes x grantii	1953
Wardiano-Hildebrandii	hildebrandii x wardianum	1902
White Dove	dearei x draconis	1947
White Gem	dicuphum x schroderianum (phal.)	1946
Wiganiae	nobile x signatum	1896
Wiganianum	hildebrandii x nobile	1901
Wilhelm Stuber	lasianthera x schroderianum (phal.)	1937
Woodlawn	atroviolaceum x spectabile	1950
Wyn Curley	infundibulum x biggibum	1963
Yellow Jacket	veratrifolium x gouldii	1951
York	nobile x regium	1963
Zillmere	superbiens x aggregatum	1962

Appendix B. List of <u>Dendrobium</u> species successfully used in primary hybrids through 1967 and their progenies.

aduncum (Eugenanthe)
x moniliforme (monile) = Aoyama

aemulum (Dendrocoryne)
x kingianum = Emmy

affine (Phalaenanthe)
x gouldii = Barbara Moore
x grantii = Alex MacKenzie
x phalaenopsis = Cascade
x strebloceras = Geo MacKenzie

aggregatum (Callista)
x superbiens = Zillmere
x undulatum = Hawaiian Sunshine

albosanguineum (Eugenanthe)
x nobile = Murrayi

anosmum (Eugenanthe)
(valid name for superbum)

antennatum (Ceratobium)
x stratiotes = Samarai

aries (Ceratobium)
x phalaenopsis = Gloucester Crimson
x superbiens = Punaluu
x taurinum = Janice Tanaka
x undulatum = Marietta Chang
x veratrifolium = Dana

atroviolaceum (Latourea)
x brymerianum = Atro-Brymerianum
x forbesii = Nellie Slade
x macrophyllum = New Guinea
x spectabile = Woodlawn

aureicolor
x phalaenopsis = Corella

aureum (Eugenanthe)
(invalid name for heterocarpum)
x findlayanum = Schneiderianum
x linawianum = Dulce
x luteolum = Cheltenhamense
x moniliforme (monile) = Endocharis

Appendix B. (Continued) List of <u>Dendrobium</u> species successfully used in primary hybrids through 1967 and their progenies.

x nobile = Ainsworthii
x regium = Royal Princess
x signatum = Ophir
x superbum (anosmum) = Gemma

barbatulum (Latourea)
x chlorops = Barbatulo-Chlorops

bensoniae (Eugenanthe)
x crystallinum = Statterianum
x macCarthiae = Kenneth
x moniliforme (monile) = Virginia
x nobile = Florence

bifalce (Latourea)
x phalaenopsis = Dalvey

biggibum (Phalaenanthe)
x d'Albertsii = Albertine
x infundibulum = Wyn Curley
x mirbellianum = Princess Stephanie
x phalaenopsis = Orchidwood
x schroderianum (phal.) = Boissyense
x strebloceras = Juweeltje
x superbiens = Saskia
x taurinum = Leahi
x toftii = Australia
x veratrifolium = Helen Park

bronckartii (Callista)
x thyrsiflorum = Mousmee

brymerianum (Eugenanthe)
x atroviolaceum = Atro-Brymerianum
x dalhousieanum (pulchellum) = Arthur Ashworth
x nobile = Hunteri

canaliculatum (Eleutheroglossum)
x d'Albertsii = Lowana Nioka
x dicuphum = Judy Leroy
x mirbellianum = Gloucester Dawn
x phalaenopsis = Rosy Tips
x undulatum = Gloucester Sands
x veratrifolium = Gloucester Charm

capra (Ceratobium)
x phalaenopsis = Ida Ann

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

chlorops (Latourea)
x barbatulum = Barbatulo-Chlorops

chrysotoxum (Callista)
x dalhousieanum (Pulchellum) = Illustre
x thyrsiflorum = Obscurum

clavatum (Eugenanthe)
x moschatum = Barbara Gittens

compactum (Phalaenanthe)
(invalid name for phal. var. compactum)
x williamsianum = Aitkenvale

crassinode (Eugenanthe)
x findlayanum = Cypheri
x linawianum = Sybil
x luteolum = Astraea
x regium = Edinense
x wardianum = Crassinode-Wardianum

crepidatum (Eugenanthe)
x nobile = Crepidato-Nobile

crystallinum (Eugenanthe)
x bensoniae = Statterianum
x moniliforme (monile) = Aeneas
x superbum (anosmum) = Francesco Allavena

d'Albertsii (Ceratobium)
x biggibum = Albertine
x canaliculatum = Lowana Nioka
x johannis = Red Wings
x mirbellianum = Moses Mark
x schroderianum (phal.) = Sarie Marijs
x undulatum = Verninha
x veratrifolium = Mount Waialeale

dalhousieanum (Eugenanthe)
(invalid name for pulchellum)
x brymerianum = Arthur Ashworth
x chrysotoxum = Illustre
x fimbriatum = Hanburyi
x formosum = Franklin W. Gamble
x moniliforme (monile) = Stratius
x nobile = Dalhou-Nobile
x superbum (anosmum) = Porphyrogastrum
x thyrsiflorum = Triumph
x undulatum = Klong Rai

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

dearei (Nigrohirsutae)
x draconis = White Dove
x formosum = Nelly Sander
x infundibulum = Thistledown
x sanderae = Isabel Sander
x schutzei = Jane Warne
x superbum (anosmum) = Emily Brant

delicatum (Dendrocoryne)
x goldiei (superbiens) = Elsie Cox
x kingianum = Gillian Leaney
x speciosum = Jane Leaney

demmenii (Ceratobium)
x schroderianum (phal.) = Tom Von Hagt

dicuphum (Phalaenanthe)
x canaliculatum = Judy Leroy
x schroderianum (phal.) = White Gem
x tokai = Tocuphum
x undulatum = Chieno

draconis (Nigrohirsutae)
x dearei = White Dove

falconeri (Eugenanthe)
x aureum (heterocarpum) = Benita
x moniliforme (monile) = Vannerianum
x nobile = Venus

falcorostrum (Dendrocoryne)
x kingianum = Bardo Rose
x speciosum = Andrew Persson

farmeri (Callista)
x thyrsiflorum = Farmeri-Thyrsiflorum

fimbriatum (Eugenanthe)
x dalhousieanum (pulchellum) = Hanburyi
x nobile = Mantinii

findlayanum (Eugenanthe)
x aureum (heterocarpum) = Schneiderianum
x crassinode = Cypheri
x hildebrandii = Mrs. Alfred Rogers
x linawianum = Harold
x nobile = Cybele
x signatum = Clarense
x wardianum = Findlayo-Wardianum

Appendix B. (Continued) List of <u>Dendrobium</u> species successfully used in primary hybrids through 1967 and their progenies.

flaviflorum (Eugenanthe)
x moschatum = Orgon

fleischeri
x schroderianum (phal.) = Pax
x stratiotes = Ong Siew Hong

forbesii (Latourea)
x atroviolaceum = Nellie Slade
x johnsoniae = Aropa

formosum (Nigrohirsutae)
x dalhousieanum (phal.) = Franklin W. Gamble
x dearei = Nelly Sander
x infundibulum = Formidible
x lowii = Formoso-Lowii
x ovipositoriferum = John Nauen
x schutzei = Sea Bird

goldiei (Phalaenanthe)
(invalid name for superbiens var. goldiei)
x delicatum = Elsie Cox
x gouldii = Tan Ghim Kheng
x johannis = Three Star
x mirbellianum = Moira Stewart
x phalaenopsis = Gregor Duruty
x tokai = Bluebird
x undulatum = Dang Toi
x veratrifolium = Calvin Morioka

gouldii (Ceratobium)
x affine = Barbara Moore
x goldiei (superbiens) = Tan Ghim Kheng
x grantii = Leah Dietz
x mirbellianum = Puhala
x phalaenopsis = Jaquelyn Thomas
x schulleri = Mem. Gordon Hew
x stratiotes = Lum Goo
x superbiens = Kapalama
x taurinum = T. Shioi
x toftii = Karen Okamoto
x tokai = Saro Roig
x undulatum = Kakela
x veratrifolium = Yellow Jacket

gracilicaule (Dendrocoryne)
x gracillum = Shan Leaney

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

gracillum (Dendrocoryne)
x gracilicaule = Shan Leaney

grantii (Ceratobium)
x affine = Alex MacKenzie
x gouldii = Leah Dietz
x johannis = Audrey Chinn
x lasianthera = Frederick G. Krauss
x phalaenopsis = Neo-Hawaii
x schulleri = Erma Jean
x stratiotes = Walter Carter
x strebloceras = Neoh Teik-Hong
x taurinum = Oahu
x veratrifolium = Verigrant

hercoglossum (Eugenanthe)
(invalid name for linguella)
x moniliforme (monile) = Isis

heterocarpum (Eugenanthe)
(valid name for aureum)

hildebrandii (Eugenanthe)
x aureum (heterocarpum) = Elwesii
x findlayanum = Mrs. Alfred Rogers
x nobile = Wiganianum
x wardianum = Wardiano-Hildebrandii

infundibulum (Nigrohirsutae)
x biggibum = Wyn Curley
x dearei = Thistledown
x formosum = Formidible
x sanderae = Infunderae

johannis (Ceratobium)
x d'Albertsii = Red Wings
x goldiei (superbiens) = Three Star
x grantii = Audrey Chinn
x mirbellianum = Kaipu
x phalaenopsis = David Baver
x senile = Kaimuki
x stratiotes = Sylvia Morley
x toftii = Tusco

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

johnsoniae (Latourea)
x forbesii = Aropa
x phalaenopsis = Bougainville
x stratiotes = Kokoda Trail

kingianum (Dendrocoryne)
x aemulum = Emmy
x delicatum = Gillian Leaney
x falcorostrum = Bardo Rose
x speciosum = Specio-Kingianum
x tetragonum = Ellen

lasianthera (Ceratobium)
x grantii = Frederick G. Krauss
x macrophyllum = Kona
x schroderianum (phal.) = Wilhem Stuber
x superbiens = Rudolf Lieske
x undulatum = Constance
x veratrifolium = Tan Chye Siam

leporinum (Ceratobium)
x phalaenopsis = Rose Marie

linawianum (Eugenanthe)
x aureum (heterocarpum) = Dulce
x crassinode = Sybil
x findlayanum = Harold
x nobile = Dominianum
x signatum = Myra
x wardianum = Chlorostele

linguella (Eugenanthe)
(valid name for hercoglossum)

lituiflorum (Eugenanthe)
x nobile = Corningianum
x wardianum = Micans

lowii (Nigrohirsutae)
x formosum = Formoso-Lowii
x sculptum = Radians

luteolum (Eugenanthe)
x aureum (heterocarpum) = Cheltenhamense
x crassinode = Astraea
x wardianum = Bryan

Appendix B. (Continued) List of <u>Dendrobium</u> species successfully used in primary hybrids through 1967 and their progenies.

macCarthiae (Eugenanthe)
- x bensoniae = Kenneth
- x moniliforme (monile) = Mac-Jap

macrophyllum (Latourea)
- x atroviolaceum = New Guinea
- x lasianthera = Kona
- x phalaenopsis = Lily Doo
- x schulleri = Golden Mac
- x stratiotes = Marguerite K. Ashford
- x superbiens = Gracia Lewis
- x undulatum = Caprice

mirbellianum (Ceratobium)
- x biggibum = Princess Stephanie
- x canaliculatum = Gloucester Dawn
- x d'Albertsii = Moses Mark
- x goldiei (superbiens) = Moira Stewart
- x gouldii = Puhala
- x johannis = Kaipu
- x schroderianum (phal.) = Roger Sander
- x schulleri = Olive
- x undulatum = Champagne

moniliforme (Eugenanthe)
(invalid name for monile)
- x aduncum = Aoyama
- x aureum (heterocarpum) = Endocharis
- x bensoniae = Virginia
- x crystallinum = Aeneas
- x dalhousieanum (pulchellum) = Stratius
- x falconeri = Vannerianum
- x hercoglossum (linguella) = Isis
- x macCarthiae = Mac-Jap
- x nobile = Cassiope
- x wardianum = Veitchii

moschatum var. cupreum
- x clavatum = Barbara Gittens
- x flaviflorum = Orgon
- x phalaenopsis = Kukui

nobile (Eugenanthe)
- x albosanguineum = Murrayi
- x aureum (heterocarpum) = Ainsworthii
- x bensoniae = Florence
- x brymerianum = Hunteri
- x crepidatum = Crepidato-Nobile

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

x dalhousieanum (pulchellum) = Dalhou-Nobile
x falconeri = Venus
x fimbriatum = Mantinii
x findlayanum = Cybele
x hildebrandii = Wiganianum
x linawianum = Dominianum
x lituiflorum = Corningianum
x moniliforme (monile) = Cassiope
x primulinum = Rolfeae
x regium = York
x ruckeri = Roeblingianum
x sanderae = Snow White
x signatum = Wiganiae
x suavissimum (chrysotoxum) = Lotus
x thwaitesiae = Variabilis
x thyrsiflorum = Backhousei
x tortile = Niobe
x wardianum = Murrhiniacum

odoardii (Ceratobium)
x undulatum = Maureen Jansen

ostrinoglossum (Ceratobium)
x phalaenopsis = Mem. Edward Trevor

ovipositoriferum (Nigrohirsutae)
x formosum = John Nauen

parishii (Eugenanthe)
x pierardii = Rhodopterygium
x superbum (anosmum) = Nestor

phalaenopsis (Phalaenanthe)
x affine = Cascade
x aries = Gloucester Crimson
x aureicolor = Corella
x bifalce = Dalvey
x biggibum = Orchidwood
x canaliculatum = Rosy Tips
x capra = Ida Ann
x goldiei (superbiens) = Gregor Duruty
x gouldii = Jaquelyn Thomas
x grantii = Neo-Hawaii
x johannis = David Baver
x johnsoniae = Bougainville
x leporinum = Rose Marie
x macrophyllum = Lily Doo

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

x moschatum = Kukui
x ostrinoglossum = Mem. Edward Trevor
x schulleri = Lim Tar Fang
x stratiotes = E. P. Boyle
x superbiens = Leeanum
x taurinum = Bangkok
x tetragonum = Suzanne
x toftii = Colin Potter
x tokai = Hawaii
x undulatum = Pauline
x veratrifolium = Veruna

pierardii (Eugenanthe)
x parishii = Rhodopterygium
x superbum (anosmum) = Adrasta

primulinum (Eugenanthe)
x nobile = Rolfeae
x superbum (anosmum) = Mentor

pulchellum (Eugenanthe)
x veratrifolium = Desaputra

pulchrum
x schroderianum (phal.) = John Laycock

regium (Eugenanthe)
x aureum (heterocarpum) = Royal Princess
x crassinode = Edinense
x nobile = York

ruckeri (Eugenanthe)
x nobile = Roeblingianum

sanderae (Nigrohirsutae)
x dearei = Isabel Sander
x infundibulum = Infunderae
x nobile = Snow White
x schutzei = Thomas Warne

sanguinolentum (Pedilonum)
x superbum (anosmum) = Rhodostoma

Appendix B. (Continued) List of <u>Dendrobium</u> species successfully used in primary hybrids through 1967 and their progenies.

schroderianum (Phalaenanthe)
(invalid name for phalaenopsis)
x biggibum = Boissyense
x d'Albertsii = Sarie Marijs
x dicuphum = White Gem
x fleischeri = Pax
x lasianthera = Wilhelm Stuber
x mirbellianum = Roger Sander
x pulchrum = John Laycock
x schulleri = Ruth Thomas
x stratiotes = Caesar
x strebloceras = Clara Cooper
x superbiens = Louis Bleriot
x taurinum = Sander's Crimson
x toftii = David Sander
x tokai = Jean Sutton
x undulatum = Püppchen
x veratrifolium = Louisae
x violaceoflavens = Arcuatum

schulleri (Ceratobium)
x gouldii = Mem. Gordon Hew
x grantii = Erma Jean
x macrophyllum = Golden Mac
x mirbellianum = Olive
x phalaenopsis = Lim Tar Fang
x schroderianum (phal.) = Ruth Thomas
x stratiotes = Bangkhen
x strebloceras = Mary Kong
x taurinum = Jessie Pung
x tokai = Arno
x trilamellatum = Ngadiman
x undulatum = Alice Noda
x veratrifolium = Vera Bong
x violaceoflavens = Charm Devi

schutzei (Nigrohirsutae)
x dearei = Jane Warne
x formosum = Sea Bird
x sanderae = Thomas Warne

sculptum (Nigrohirsutae)
x lowii = Radians

senile (Eugenanthe)
x johannis = Kaimuki

Appendix B. (Continued) List of <u>Dendrobium</u> species successfully used in primary hybrids through 1967 and their progenies.

signatum (Eugenanthe)
- x aureum (heterocarpum) = Ophir
- x findlayanum = Clarense
- x linawianum = Myra
- x nobile = Wiganiae

speciosum (Dendrocoryne)
- x delicatum = Jane Leaney
- x falcorostrum = Andrew Persson
- x kingianum = Specio-Kingianum

spectabile (Latourea)
- x atroviolaceum = Woodlawn

stratiotes (Ceratobium)
- x antennatum = Samarai
- x fleischeri = Ong Siew Hong
- x gouldii = Lum Goo
- x grantii = Walter Carter
- x johannis = Sylvia Morley
- x johnsoniae = Kokoda Trail
- x macrophyllum = Marguerite K. Ashford
- x phalaenopsis = E. P. Boyle
- x schroderianum (phal.) = Caesar
- x schulleri = Bangkhen
- x strebloceras = Devesianum
- x superbiens = Queensland
- x taurinum = Varsity
- x toftii = Lisa Ann
- x tokai = Strattokai
- x undulatum = Salak
- x veratrifolium = Sunda Islands
- x violaceoflavens = Morgenster
- x williamsianum = Milne Bay

strebloceras (Ceratobium)
- x affine = Geo MacKenzie
- x biggibum = Juweeltje
- x grantii = Neoh Teik-Hong
- x schroderianum (phal.) = Clara Cooper
- x schulleri = Mary Kong
- x stratiotes = Devesianum

suavissimum (Callista)
(invalid name for chrysotoxum var. suavissimum)
- x nobile = Lotus

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

superbiens (Phalaenanthe)
x aggregatum = Zillmere
x aries = Punaluu
x biggibum = Saskia
x gouldii = Kapalama
x lasianthera = Rudolf Lieske
x macrophyllum = Gracia Lewis
x phalaenopsis = Leeanum
x schroderianum (phal.) = Louis Bleriot
x stratiotes = Queensland
x taurinum = Kauai
x toftii = Blue Gloucester
x undulatum = Albanense
x veratrifolium = Brisbane
x violaceoflavens = Phyllis

superbum (Eugenanthe)
(invalid name for anosmum)
x aureum (heterocarpum) = Gemma
x crystallinum = Francesco Allavena
x dalhousieanum (pulchellum) = Porphyrogastrum
x dearei = Emily Brant
x parishii = Nestor
x pierardii = Adrasta
x primulinum = Mentor
x sanguinolentum = Rhodostoma

taurinum (Ceratobium)
x aries = Janice Tanaka
x biggibum = Leahi
x gouldii = T. Shioi
x grantii = Oahu
x phalaenopsis = Bangkok
x schroderianum (phal.) = Sander's Crimson
x schulleri = Jessie Pung
x stratiotes = Varsity
x superbiens = Kauai
x tokai = Shibata
x undulatum = Taurus
x veratrifolium = 442nd Infantry

tetragonum (Dendrocoryne)
x kingianum = Ellen
x phalaenopsis = Suzanne

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

thyrsiflorum (Callista)
- x chrysotoxum = Obscurum
- x dalhousieanum = Triumph
- x farmeri = Farmeri-Thyrsiflorum
- x nobile = Backhousei

toftii (Ceratobium)
- x biggibum = Australia
- x gouldii = Karen Okamoto
- x johannis = Tusco
- x phalaenopsis = Colin Potter
- x schroderianum (phal.) = David Sander
- x stratiotes = Lisa Ann
- x superbiens = Blue Gloucester
- x undulatum = Peter Petersen
- x veratrifolium = Rickie Cornetti
- x williamsianum = Kila Blue

tokai (Ceratobium)
- x dicuphum = Tocuphum
- x goldiei (superbiens) = Bluebird
- x gouldii = Saro Roig
- x phalaenopsis = Hawaii
- x schroderianum (phal.) = Jean Sutton
- x schulleri = Arno
- x stratiotes = Strattokai
- x taurinum = Shibata
- x undulatum = Alice Spalding
- x veratrifolium = Joanne Sawers

tortile (Eugenanthe)
- x nobile = Niobe

trilamellatum (Ceratobium)
- x schulleri = Ngadiman
- x undulatum = Rosalind Choon Lin

undulatum (Ceratobium)
- x aggregatum = Hawaiian Sunshine
- x aries = Marietta Chang
- x canaliculatum = Gloucester Sands
- x d'Albertsii = Verninha
- x dalhousieanum (pulchellum) = Klong Rai
- x dicuphum = Chieno
- x goldiei (superbiens) = Dang Toi
- x gouldii = Kakela
- x lasianthera = Constance
- x macrophyllum = Caprice

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

x mirbellianum = Champagne
x odoardi = Maureen Jansen
x phalaenopsis = Pauline
x schroderianum (phal.) = Püppchen
x schulleri = Alice Noda
x stratiotes = Salak
x superbiens = Albanense
x taurinum = Taurus
x toftii = Peter Petersen
x tokai = Alice Spalding
x trilamellatum = Rosalind Choon Lin
x veratrifolium = Ursula
x violaceoflavens = Medusa

veratrifolium (Ceratobium)
x aries = Dana
x biggibum = Helen Park
x canaliculatum = Gloucester Charm
x d'Albertsii = Mount Waialeale
x goldiei (superbiens) = Calvin Morioka
x gouldii = Yellow Jacket
x grantii = Verigrant
x lasianthera = Tan Chye Siam
x phalaenopsis = Veruna
x pulchellum = Desaputra
x schroderianum = Louisae
x schulleri = Vera Bong
x stratiotes = Sunda Islands
x superbiens = Brisbane
x taurinum = 442nd Infantry
x toftii = Rickie Cornetti
x tokai = Joanne Sawers
x undulatum = Ursula

violaceoflavens (Ceratobium)
x schroderianum (phal.) = Arcuatum
x schulleri = Charm Devi
x stratiotes = Morgenster
x superbiens = Phyllis
x undulatum = Medusa

wardianum (Eugenanthe)
x aureum (heterocarpum) = Aspasia
x crassinode = Crassinode-Wardianum
x findlayanum = Findlayanum-Wardianum
x hildebrandii = Wardiano-Hildebrandii
x linawianum = Chlorostele
x lituiflorum = Micans

Appendix B. (Continued) List of Dendrobium species successfully used in primary hybrids through 1967 and their progenies.

x luteolum = Bryan
x moniliforme (monile) = Veitchii
x nobile = Murrhiniacum

williamsianum (Ceratobium)
x compactum (phal.) = Aitkenvale
x stratiotes = Milne Bay
x toftii = Kila Blue

Appendix C. Number of *Dendrobium* primary hybrids registered through 1967, listed according to sections crossed.

Sections Crossed	Number of Primary Hybrids Registered
Eugenanthe x Eugenanthe	63
Ceratobium x Ceratobium	60
Ceratobium x Phalaenanthe	53
Nigrohirsutae x Nigrohirsutae	12
Phalaenanthe x Phalaenanthe	8
Dendrocoryne x Dendrocoryne	8
Ceratobium x Latourea	5
Latourea x Latourea	5
Latourea x Phalaenanthe	4
Callista x Eugenanthe	4
Ceratobium x Eleutheroglossum	4
Ceratobium x Eugenanthe	3
Callista x Callista	3
Eugenanthe x Nigrohirsutae	2
Eleutheroglossum x Phalaenanthe	2
Eugenanthe x Latourea	1
Dendrocoryne x Phalaenanthe	2
Callista x Ceratobium	1
Eugenanthe x Phalaenanthe	1
Eugenanthe x Pedilonum	1
Callista x Phalaenanthe	1
Nigrohirsutae x Phalaenanthe	1
Unclassifiable at present	4
Total	248

Appendix D. Dendrobium sectional classification systems of R. Schlechter (1912) and F. Kraenzlin (1910).

Schlechter	Kraenzlin
Dendrobium	Dendrobium
Desmotrichum	I. Eudendrobium
Microphytanthe	A. Biflora
Goniobulbon	1. Nobilia
Diplocaulobium	2. Aurea
Bolbidium	3. Aquea
Euphlebium	4. Stuposa
Rhizobium	5. Macrostachya
Sarcopodium	B. Racemosa
Dendrocoryne	1. Chrysotoxa
Latourea	2. Aniospetala
Inobulbon	3. Herbacea
Callista	4. Stachyobia
Eugenanthe	II. Nigro-hirsuta
Platycaulon	III. Pedilonum
Pedilonum	A. Secunda
Calyptrochilus	B. Glomerata
Cuthbertsonia	C. Capitata
Oxyglossum	D. Ceratobium
Brachyanthe	E. Brevisaccata
Stachyobium	IV. Grastidium
Fytchianthe	A. Conostalix
Phalaenanthe	B. Bambusacea
Eleutheroglossum	C. Revoluta
Ceratobium	D. Eugrastidium
Trachyrhizum	V. Aporum
Distichophyllum	A. Hemiphylla
Oxygenianthe	B. Holophylla
Amblyanthus	VI. Strongyle
Kinetochilus	VII. Crumenata
Rhopalanthe	VIII. Dendrocoryne
Aporum	A. Tokai
Oxystophyllum	B. Trachytheca
Grastidium	C. Leiotheca
Dichopus	D. Superbientia
Eriopexis	E. Euphlebia
Pleianthe	F. Platycaula
Macrocladium	G. Speciosa
Dolichocentrum	Related Genera
Conostalix	Callista
Monanthos	Inobulbon
Herpethophytum	Sarcopodium
	Diplocaulobium
	Desmotrichum

Appendix E. Culture medium for orchid seeds and seedlings, modified from Knudson's C (1946) medium.

Chemical Name	Chemical Formula	Amount
Ammonium sulfate	$(NH_4)_2SO_4$	2.000 g
Calcium nitrate	$Ca(NO_3)_2$	1.000 g
Potassium chloride	KCl	1.000 g
Potassium phosphate monobasic	KH_2PO_4	0.250 g
Magnesium sulfate	$MgSO_4$	0.250 g
Ferrous sulfate	$FeSO_4$	0.050 g
Manganous sulfate	$MnSO_4$	0.015 g
Bacteriological peptone	-----	4.000 g
Agar-agar	-----	17.000 g
Sucrose	$C_6H_{12}O_{11}$	40.000 g
Coconut water	-----	500.000 ml
Distilled water	H_2O	1500.000 ml

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