Chromosome Homology in the Ceratobium, Phalaenanthe, and Latourea Sections of the Genus *Dendrobium*[1]

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THE *Dendrobium* genus comprises over 1,000 species of epiphytic orchids distributed over a vast triangular area connecting India, New Zealand, and Japan, and including most of the tropical and subtropical land areas between 60 and 180 east longitude. This large genus has been subdivided into numerous sections on the basis of morphological characteristics (Holttum, 1957). Members of the Ceratobium, Phalaenanthe, and Latourea sections are distributed in New Guinea and surrounding areas. Both Ceratobium and Latourea are represented by at least 30 species each, while Phalaenanthe includes a relatively few species. Several species in these sections have been widely cultivated and extensively hybridized to produce the improved and popular horticultural varieties of today.

Cytological investigations to date have revealed 2n = 38 for all species in Ceratobium, Phalaenanthe, and Latourea sections, and both 2n = 38 and 40 in other sections but with 38 predominating (Ito and Mutsuura, 1957; Kosaki, 1958; Vajrabhaya and Randolph, 1961; Kosaki and Kamemoto, 1962). Thus divergence of species in the genus appears to have been accompanied by little or no change in chromosome number.

During the past 2 decades, numerous intra- and intersectional species hybrids in *Dendrobium* have been produced by various orchid hybridizers. Since cytological studies, particularly observations on chromosome homology, are very useful in elucidating taxonomic and phylogenetic relationships, as well as in aiding the breeding of orchids, the present investigation was initiated to examine the meiotic behavior of all available species and hybrids involving the Ceratobium, Phalaenanthe, and Latourea sections, and to establish the relationships of species of these groups.

MATERIALS AND METHODS

The species involved in this study are listed in Table 1 along with their geographical distribution, while the hybrids with their registered names are found in Table 2. Plants were obtained from the Foster Botanical Garden and orchid nurseries in Honolulu. Young pollinia were sliced and fixed in 1:1:2 mixture of chloroform, 95% ethyl alcohol, and glacial acetic acid for 20-30 min at room temperature. They were then transferred to 45% acetic acid for 20-30 min to soften the tissue and promote the stainability of chromosomes. They were then squashed and stained in 1% aceto-orcein.

OBSERVATIONS

Meiosis in Species

Meiosis in 11 species representing the sections, Ceratobium, Phalaenanthe, and Latourea (Figs. 1–12) showed consistently 19 bivalent chromosomes at metaphase I (Table 3). The products of meiosis were normal tetrads with 19 chromosomes distributed in each microspore.

The bivalents were either rod or ring shape with terminalized chiasmata (Figs. 24–26). The size of bivalents differed markedly within a complement. This difference was more conspicuous in species of Ceratobium and Phalaenanthe than in Latourea. There were also distinguishable differences in the genomes of different species within the same section.

Metaphase I configurations of *D. undulatum* were characterized by the presence of conspicuously large and heteropycnotic bivalent chromosomes (Fig. 24) which were readily discernible at late prophase and metaphase of either meiosis or microspore division. These chromosomes

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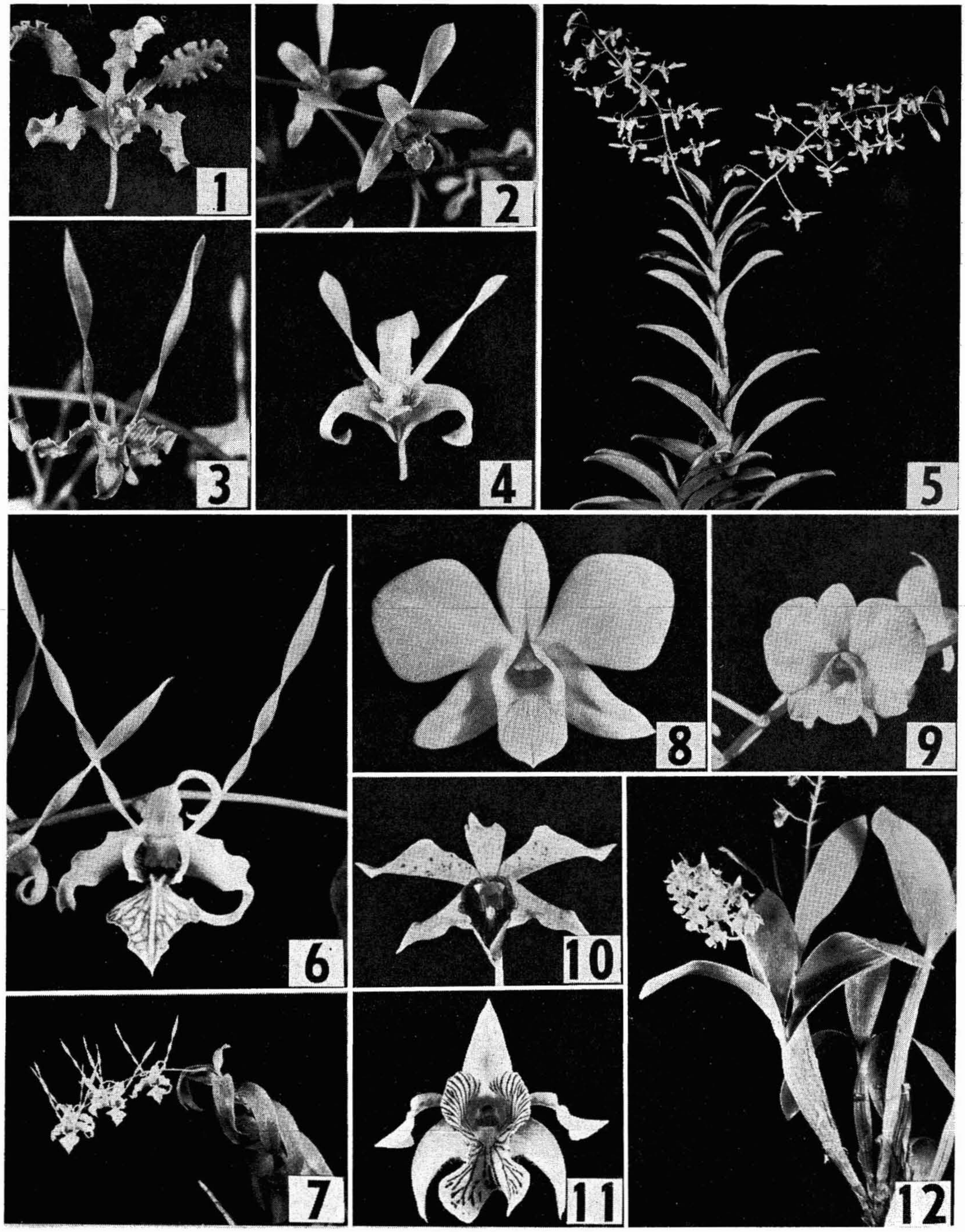


FIGS. 1–12. *Dendrobium* species (plant habit, 1/5 ×; close-up, 1 ×). 1, *D. undulatum*. 2, *D. veratrifolium*. 3, *D. strebloceras*. 4, 5, *D. grantii*. 6, 7, *D. stratiotes*. 8, *D. phalaenopsis*. 9, *D. bigibbum*. 10. *D. atroviolaceum*. 11, 12, *D. macrophyllum*.

TABLE 1

SPECIES INVESTIGATED OR INVOLVED AS PARENTS OF HYBRIDS

SECTION	SPECIES	GEOGRAPHICAL DISTRIBUTION
Ceratobium	*D. gouldii* Rchb. f.	Thursday Island
	D. grantii C. T. White	New Guinea
	D. Johannis Rchb. f.*	Northern Queensland, Thursday Island
	D. lasianthera J. J. S.*	New Guinea
	D. mirbelianum Gaud.*	New Guinea
	D. schulleri J. J. S.*	New Guinea
	D. stratiotes Rchb. f.	Celebes
	D. strebloceras Rchb. f.	Sunda Islands
	D. taurinum Lindl.*	Philippines
	D. tokai Rchb. f.	Fiji
	D. undulatum R. Br.	Northern Queensland, New Guinea
	D. veratrifolium Lindl.	New Guinea
Phalaenanthe	*D. bigibbum* Lindl.	Cape York Peninsula, New Guinea
	D. phalaenopsis Fitzg.	Moluccas to northern Queensland
Latourea	*D. atroviolaceum* Rolfe*	New Guinea
	D. macrophyllum Lindl.	New Guinea to Java

* Involved as a parent of hybrid investigated.

might well serve as "markers" for the genome of *D. undulatum*.

D. strebloceras possessed two pairs of chromosomes which were larger in size than the rest of the complement and were strongly heteropycnotic at prophase of meiosis. *D. stratiotes* showed similar characteristics, but with additional pairs of large bivalents. *D. veratrifolium*, *D. phalaenopsis* (Fig. 25) and others also possessed several large bivalents but of graded size and heteropycnosis.

Meiosis in Within-Section Diploid Hybrids of Ceratobium

The 10 intrasectional diploid hybrids of Ceratobium (Figs. 13, 14) investigated showed regular pairing at meiosis (Table 4). However, some of the bivalents were conspicuously heteromorphic. This might be expected on the basis of the morphological variations of chromosomes of the different genomes.

The number and form of heteromorphic pairs varied from one hybrid to another depending on the parentage. The two hybrids of *D. undulatum*—*D. veratrifolium* x *D. undulatum* and *D. undulatum* x *D. gouldii*—showed a markedly heteromorphic bivalent involving the large "marker" chromosome of *D. undulatum*. Highly heteromorphic bivalents were also observed in *D. stratiotes* hybrids. Four such bivalents were observed for *D. stratiotes* x *D. tokai*, and four to five in *D. veratrifolium* x *D. stratiotes* (Fig. 27). The smaller of the bivalent chromosomes often appeared as a chromatin thread pulled out from the darkly stained larger chromosome. These bivalents characteristically separated precociously.

Meiosis in Between-Section Diploid Hybrids of Phalaenanthe and Ceratobium

In addition to the natural hybrid, *D. superbiens* (Figs. 17, 18), six diploid intersectional hybrids involving Phalaenanthe and Ceratobium (Figs. 15, 16) exhibited similarly irregular meiotic behavior (Tables 5, 9, Figs. 28, 29). Both bivalents and univalents were observed, and occasionally some trivalents probably resulting from the chance association of sticky chromosomes were also seen.

The bivalents in PMCs varied in number from 19 to 13 and the univalents from 2 to 12. Most of the PMCs formed 19–16 bivalents and 0–6 univalents. As indicated in Table 5, the mean number of bivalents was highest (18.9)

TABLE 2

HYBRIDS INVESTIGATED

SECTION	SPECIES CROSSED	REGISTERED NAME
Ceratobium x Ceratobium	*D. veratrifolium* x *D. undulatum*	*D.* ursula
	D. veratrifolium x *D. stratiotes*	*D.* Sunda Island
	D. veratrifolium x *D. tokai*	*D.* Joanne Sawers
	D. veratrifolium x *D. schulleri*	(Not registered)
	D. veratrifolium x *D.* Taurus*	*D.* 100th Battalion
	D. stratiotes x *D. tokai*	*D.* stratokai
	D. stratiotes x *D. undulatum*	*D.* Salak
	D. undulatum x *D. gouldii*	*D.* Kakela
	D. taurinum x *D. gouldii*	*D.* T Shioi
	D. mirbelianum x *D. Johannis*	*D.* Kaipu
Phalaenanthe x Ceratobium	*D. superbiens* (natural hybrid)	
	D. phalaenopsis x *D. undulatum*	*D.* Pauline
	D. phalaenopsis x *D. gouldii*	*D.* Jaquelyn Thomas
	D. phalaenopsis x *D. tokai*	*D.* Hawaii
	D. phalaenopsis x *D. taurinum*	*D.* Sanders Crimson
	D. phalaenopsis x *D. Johannis*	*D.* David Baver
	D. phalaenopsis x *D. veratrifolium*	*D.* Luisea
Latourea x Latourea	*D. atroviolaceum* x *D. macrophyllum*	*D.* New Guinea
Ceratobium x Latourea	*D. lasianthera* x *D. macrophyllum*	*D.* Kona
Phalaenanthe x Latourea	*D. phalaenopsis* x *D.* New Guinea	*D.* 50th State

* *D.* Taurus = *D. taurinum* x *D. undulatum.*

in *D. phalaenopsis* x *D. johannis,* and disclosed a rather strong homology of the parental genomes. *D. phalaenopsis* x *D. taurinum* also showed a high degree of metaphase pairing. A relatively low mean number of bivalents (15.7) was exhibited by *D. phalaenopsis* x *D. gouldii.* A second plant of the same cross also produced a relatively low number of bivalents (17.1). Other hybrids averaged from 17.7 to 17.8 bivalents.

Excepting *D. superbiens,* all hybrids exhibited two or more extremely heteromorphic bivalents

TABLE 3

MEAN CHROMOSOME CONFIGURATIONS AT METAPHASE I OF MEIOSIS IN PMCs OF SPECIES, 2N = 38

SECTION	SPECIES	MEAN CONFIGURATION PER PMC	NUMBER OF PMCs OBSERVED
Ceratobium	*D. gouldii*	19.0 II	25
	D. grantii	19.0 II	25
	D. stratiotes	19.0 II	25
	D. strebloceras	19.0 II	25
	D. tokai	19.0 II	25
	D. undulatum	19.0 II	25
	D. veratrifolium	19.0 II	25
Phalaenanthe	*D. bigibbum*	19.0 II	25
	D. phalaenopsis	19.0 II	25
Latourea	*D. macrophyllum*	19.0 II	25

(Fig. 29) which often separated precociously. The synaptic force of the heteromorphic bivalents was weak as evidenced by the precocious separation and the frequent close proximity of large and small univalents in a metaphase figure.

D. superbiens has been considered a natural hybrid between species of the sections Phalaenanthe and Ceratobium (Holttum, 1957). Its hybrid nature can be confirmed through the meiotic irregularity which is comparable to that of other intersectional hybrids.

The products of meiosis were predominately tetrads (Table 9). These reflect the relatively high degree of chromosome pairing at meiosis. The percentage of spore tetrads was 90 or higher for all hybrids except *D. phalaenopsis* x *D. gouldii* (#2), which produced about 30% dyads and dyads with microcytes.

Meiosis in Tetraploid Hybrids

A within-section tetraploid, *D. stratiotes* x *D. undulatum* and a between-section tetraploid, *D. phalaenopsis* x *D. gouldii,* exhibited considerable difference in meiotic behavior (Table 6, Figs. 30, 31). Metaphase I configurations of the within-section tetraploid were various combinations of univalents, bivalents, and quadrivalents. The bivalents varied in number from 38 to 32, and the quadrivalents and univalents from 2 to 0. Common configurations were 1 IV + 36 II and 38 II. Quadrivalents involved the chromosomes of medium size. The two largest chromosomes which were presumed to be of *D. undulatum* origin exhibited a rather unusual behavior. They either paired with each other or, as can be seen in Figure 30, paired with small chromosomes to form the two extremely heteromorphic bivalents. The two types of pairing occurred at about equal frequencies.

The second largest pair of chromosomes presumably contributed by *D. stratiotes* also behaved in a similar fashion. The attenuation of the smaller chromosomes appeared to be a common characteristic of these extremely heteromorphic bivalents. Still other, though less conspicuous, heteromorphic bivalents varying in number from one PMC to another were also observed. These variations in pairing of chromosomes strongly suggest that autosyndetic as well as allosyndetic pairing occurs in this tetraploid hybrid involving two relatively closely related species.

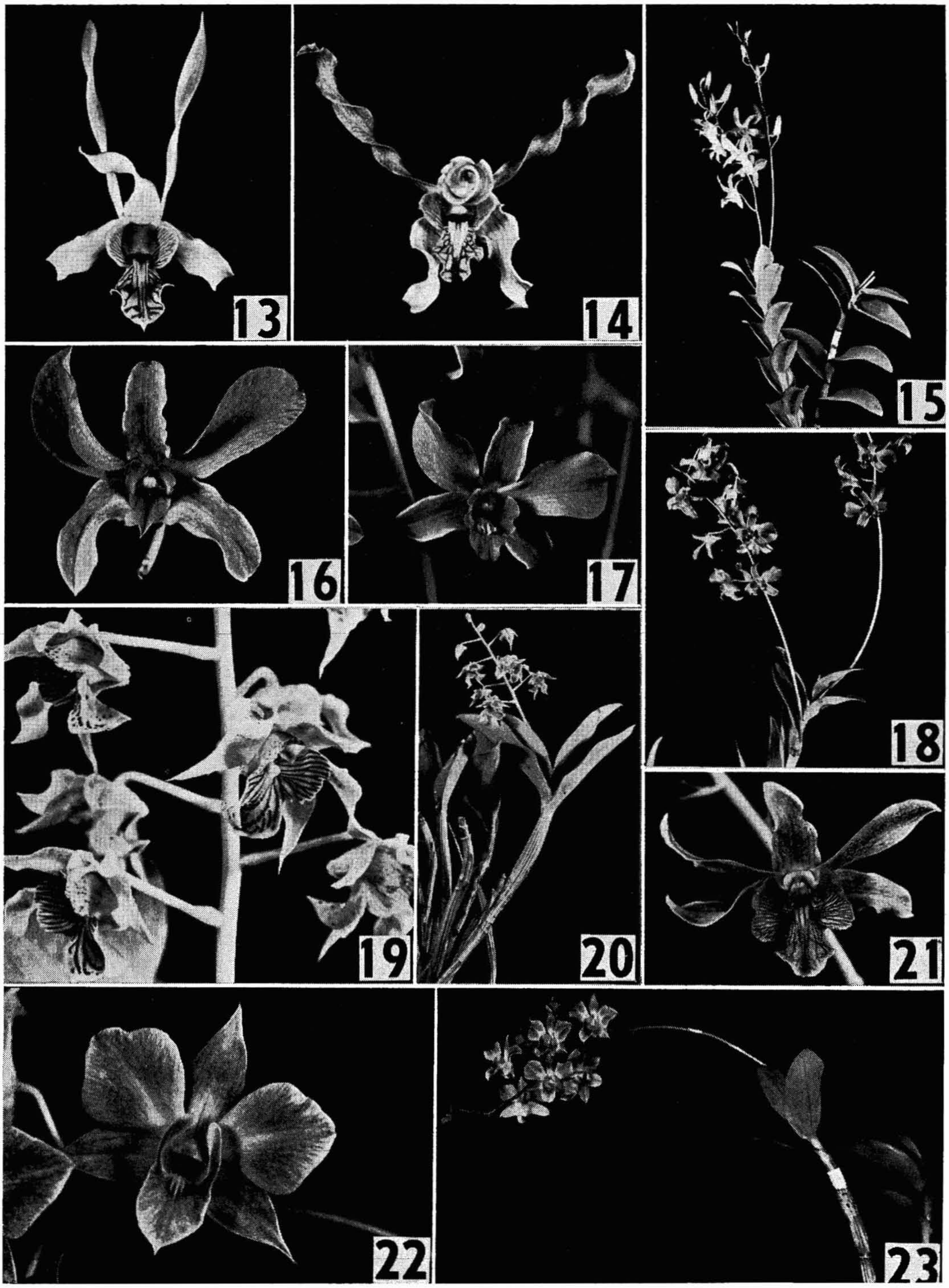
The between-section tetraploid hybrid, *D. phalaenopsis* x *D. gouldii,* showed normal meiosis with 38 bivalents, and normal tetrads of microspores. The diploid hybrid of the same cross formed 19–13 bivalent associations at meiosis, but doubling in chromosome number restored complete regularity in meiosis, thereby revealing the amphidiploid nature of the tetraploid hybrid.

TABLE 4

MEAN CHROMOSOME CONFIGURATIONS AT METAPHASE I OF MEIOSIS IN PMCs OF WITHIN-SECTION HYBRIDS OF CERATOBIUM, 2N = 38

HYBRID	MEAN CONFIGURATION PER PMC	NUMBER OF PMCs OBSERVED
D. veratrifolium x *D. undulatum,* #1	19.0 II	25
D. veratrifolium x *D. undulatum,* #2	19.0 II	25
D. veratrifolium x *D. stratiotes*	19.0 II	25
D. veratrifolium x *D. tokai*	19.0 II	25
D. veratrifolium x *D. schulleri*	19.0 II	25
D. veratrifolium x *D.* Taurus*	19.0 II	25
D. stratiotes x *D. tokai*	19.0 II	25
D. undulatum x *D. gouldii*	19.0 II	25
D. taurinum x *D. gouldii*	19.0 II	25
D. mirbelianum x *D. johannis*	19.0 II	25

* *D.* Taurus = *D. taurinum* x *D. undulatum.*



FIGS. 13–23. Dendrobium hybrids (plant habit, 1/5 ×; close-up, 1 ×). 13, *D. veratrifolium* x *D. stratiotes*. 14, *D. stratiotes* x *D. undulatum*. 15, *D. phalaenopsis* x *D. tokai*. 16, *D. phalaenopsis* x *D. undulatum*. 17, 18, *D. superbiens*. 19, 20, *D. atroviolaceum* x *D. macrophyllum*. 21, *D. lasianthera* x *D. macrophyllum*. 22, 23, *D. phalaenopsis* x *D.* New Guine.

TABLE 5

MEAN CHROMOSOME CONFIGURATIONS AT METAPHASE I OF MEIOSIS IN PMCS OF BETWEEN-SECTION HYBRIDS OF PHALAENANTHE AND CERATOBIUM, 2N = 38

HYBRID	MEAN CONFIGURATION PER PMC	NUMBER OF PMCS OBSERVED
D. superbiens (natural hybrid)	$2.04_1+17.80_2+0.12_3$	25
D. phalaenopsis x *D. undulatum*	$2.34_1+17.76_2$	29
D. phalaenopsis x *D. gouldii*, #1	$3.87_1+17.07_2$	25
D. phalaenopsis x *D. gouldii*, #2	$6.48_1+15.76_2$	25
D. phalaenopsis x *D. tokai*	$2.42_1+17.73_2+0.04_3$	26
D. phalaenopsis x *D. taurinum*	$1.00_1+18.50_2$	24
D. phalaenopsis x *D. johannis*	$0.16_1+18.92_2$	100
D. phalaenopsis x *D. veratrifolium*	$2.50_1+17.70_2+0.03_3$	30

Meiosis in Within-Section Hybrid of Latourea

The single plant of *D. atroviolaceum* x *D. macrophyllum* (Figs. 19, 20) was a rare and unexpected hypodiploid with 2n = 37. Meiotic behavior was comparable to that often encountered in trisomics (Tables 7, 9, Fig. 32). Twenty-four out of 25 PMCs examined showed one trivalent plus 17 bivalents and only 1 PMC showed 18 bivalents plus a univalent.

A few bivalents were more or less heteromorphic. Trivalents were either V-shape or, as can be seen in Figure 32, a chain of three. At anaphase I, the chromosomes of the bivalents separated regularly to both poles, while the trivalent usually separated two for one. The products of meiosis were tetrads.

Meiosis in Between-Section Hybrid of Ceratobium and Latourea

The irregular meiosis in *D. lasianthera* x *D. macrophyllum* (Fig. 21) revealed variations in number of bivalents from 14 to 7 with a mean of 10.8 and univalents from 10 to 26 with a mean of 16.3 (Table 8, Fig. 33). Nearly all bivalents were heteromorphic. Univalents were of variable size, and scattered in and around the loose metaphase plate.

At anaphase I, the bivalents separated toward both poles, while the univalents often lagged between the two anaphase groups, and ultimately the entire group was reconstituted into restitution nuclei. Dyads and dyads with microcytes were, therefore, common products of meiosis. A few triads, tetrads, and tetrads with microcytes were also observed (Table 9). The relatively high frequency of triad formation suggests that restitution also occurred at the second division.

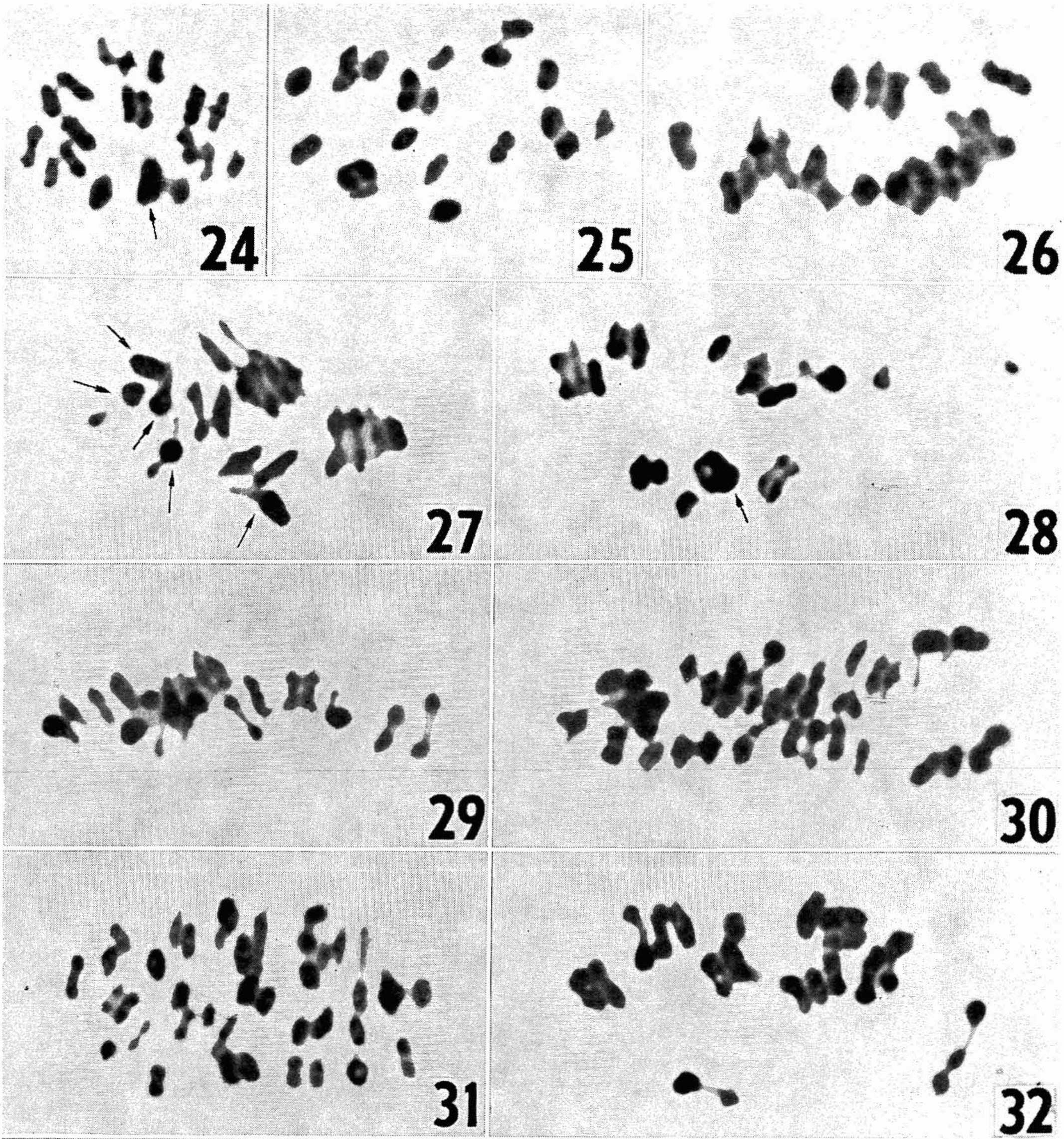
Meiosis in Between-Section Hybrid of Phalaenanthe and Latourea

Meiosis in *D. phalaenopsis* x *D.* New Guinea (Figs. 22, 23) was highly irregular. The number

TABLE 6

CHROMOSOME CONFIGURATIONS AT METAPHASE I OF MEIOSIS IN PMCS OF TETRAPLOID HYBRIDS, 2N = 76

SECTIONS INVOLVED	HYBRID	CHROMOSOME CONFIGURATIONS 38_2	1_4 37_2 2_1	1_4 36_2	1_4 35_2 2_1	2_4 34_2	2_4 33_2 2_1	2_4 32_2
Ceratobium x Ceratobium	*D. stratiotes* x *D. undulatum*	12	2	15	3	4	1	2
Phalaenanthe x Ceratobium	*D. phalaenopsis* x *D. gouldii*	25						



FIGS. 24–34. Chromosomes at metaphase I of meiosis in PMCs of species and hybrids of *Dendrobium* (2,100 ×). 24, *D. undulatum*, 19II. 25, *D. phalaenopsis*, 19II. 26, *D. macrophyllum*, 19II. 27, *D. veratrifolium* x *D. stratiotes*, 19II. 28, *D. superbiens*, 18II + 2I. 29, *D. phalaenopsis* x *D. undulatum*, 18II + 2I. 30, *D. stratiotes* x *D. undulatum*, tetraploid, 38II. 31, *D. phalaenopsis* x *D. gouldii*, tetraploid, 38II. 32, *D. atroviolaceum* x *D. macrophyllum*, 2n = 37, 1III + 17II. 33, *D. lasianthera* x *D. macrophyllum*, 12II + 14I. 34, *D. phalaenopsis* x *D.* New Guinea, 3II + 32I.

TABLE 7

CHROMOSOME CONFIGURATIONS AT METAPHASE I OF MEIOSIS IN PMCs OF A WITHIN-SECTION HYBRID OF LATOUREA, 2N = 37

HYBRID	CHROMOSOME CONFIGURATIONS		
	17_2+1_3	$2_1+16_2+1_3$	1_1+18_2
D. atroviolaceum x *D. macrophyllum*	22	2	1

of bivalents ranged from 7–0 with a mean of 1.8, and that of univalents from 23–38 (Table 8). PMCs with no bivalents and 38 univalents were common. No definite metaphase plates were formed at metaphase I (Fig. 34). The movement of chromosomes to either pole at anaphase I was not orderly enough to produce the usual daughter nuclei, and consequently restitution was common for the majority of PMCs. The products of meiosis were mostly dyads with or without microcytes, but tetrads, monads, and triads were also observed (Table 9).

DISCUSSION

Meiosis in 11 species investigated was, as one might expect, regular. Also the within-section hybrids of Ceratobium exhibited 19 bivalents regularly indicating a strong homology of species genomes within this section (Fig. 35). However, some morphological variation of chromosomes was evidenced through the formation of heteromorphic bivalents in the species hybrids. The relatively high fertility that breeders encounter in these within-section hybrids reflects the strong homology of the parental genomes.

The between-section diploid hybrids involving the Ceratobium and Phalaenanthe sections indicated a greater divergence of parental genomes, for bivalents per PMC averaged from 18.9 to 15.8. The fertility of these hybrids is generally impaired by the irregularity in metaphase pairing.

Meiosis in intra- and intersectional tetraploid hybrids throw additional light on the genome homology in Ceratobium and Phalaenanthe. The within-section tetraploid hybrid of Ceratobium, *D. stratiotes* x *D. undulatum* formed quadrivalents, bivalents, and univalents which is a characteristic chromosomal behavior of autotetraploids, while the between-section tetraploid hybrid of Ceratobium and Phalaenanthe, *D. phalaenopsis* x *D. gouldii,* behaved as a typical amphidiploid with the exclusive formation of bivalents. It might be noted that the diploid counterpart of the within-section tetraploid showed good pairing at meiosis, while the diploid counterpart of the between-section tetraploid was irregular in meiosis. The intersectional diploid hybrids are generally low in fertility due to the poor chromosome pairing at metaphase, but doubling results in regularity in meiosis and the consequent restoration of

TABLE 8

MEAN CHROMOSOME CONFIGURATIONS AT METAPHASE I OF MEIOSIS IN PMCs OF BETWEEN-SECTION HYBRIDS OF LATOUREA, 2N = 38

SECTION	SPECIES CROSSED	MEAN CONFIGURATION PER PMC	NUMBER OF PMCs OBSERVED
Ceratobium x Latourea	*D. lasianthera* x *D. macrophyllum*	$16.31_1+10.83_2$	30
Phalaenanthe x Latourea	*D. phalaenopsis* x *D.* New Guinea*	$34.28_1+1.81_2+0.32_3$	31

* *D.* New Guinea is *D. atroviolaceum* x *D. macrophyllum*.

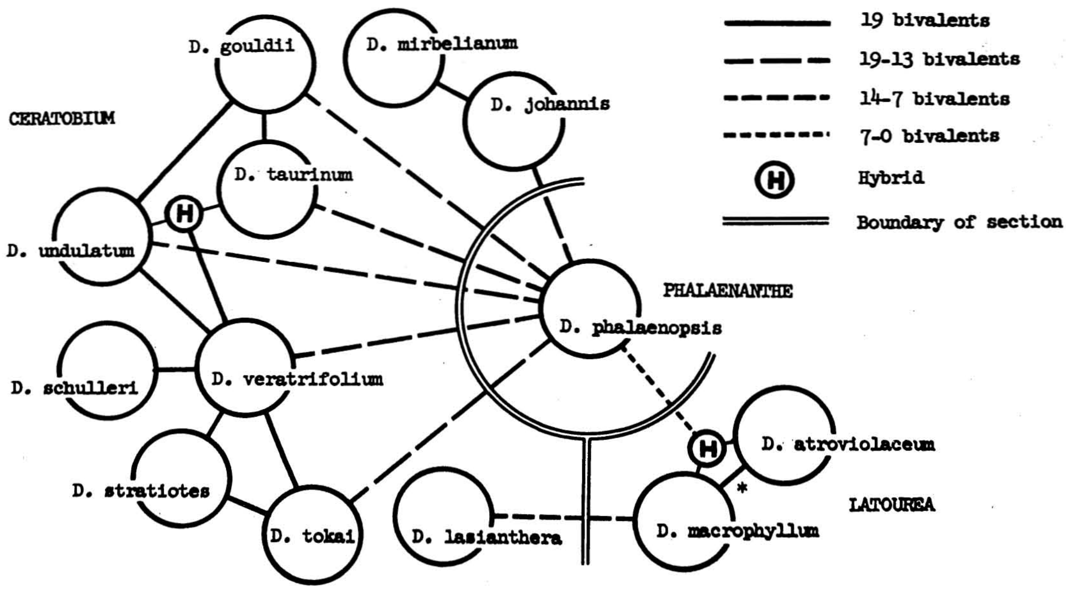


FIG. 35. Diagrammatic representation of chromosome homology in hybrids of *Dendrobium*. The hybrid investigated was a monosomic.

fertility. On the other hand, tetraploidy in intrasectional hybrids results in reduced fertility due to the homologous parental genomes forming multivalents.

D. superbiens was originally given species status but now it is generally recognized as a natural hybrid between species from the sections Phalaenanthe and Ceratobium (Holttum, 1957). The intersectional hybrid, *D. phalaenopsis* x *D. undulatum* most closely resemble *D. superbiens* in external morphology, but the large "marker" chromosome of *D. undulatum* was conspicuously absent in the particular plant examined. Further studies involving several individual plants collected from their natural habitat should clarify the cytological aspects of this natural hybrid.

It appears that the taxonomic gap between Ceratobium and Latourea is much wider than that between Ceratobium and Phalaenanthe (Fig. 35), for the Ceratobium-Latourea hybrid exhibited an average of 10.8 bivalents per PMC, while the Ceratobium-Phalaenanthe hybrids averaged between 18.9 to 15.8. The gap between Phalaenanthe and Latourea is still greater as indicated by the very weak homology of parental genomes forming an average of only 1.8 bivalents per PMC.

The separation of species into the three groups, Ceratobium, Phalaenanthe, and Latourea appears to be valid on the basis of external morphology, cytology, or crossability. Ceratobium and Phalaenanthe are phylogenetically much more closely related to each other than they are to Latourea. Also, it might be concluded that Latourea is more closely related to Ceratobium than to Phalaenanthe. If evolution of these groups occurred in a sequential manner, then it is logical to assume that divergence proceeded from Latourea to Ceratobium to Phalaenanthe.

Considerable differences in taxonomy and phylogeny might be noted for the *Dendrobium* genus and the *Vanda* alliance. Holttum (1957) has pointed out that:

> The flower-form throughout the tribe (Dendrobium) is remarkably constant; there is much greater variation in vegetative characters. This is an interesting contrast to the Vanda-Arachnis tribe, in which floral form is very varied and vegetative form much less so.

> Botanists always consider flower-characters more important than vegetative ones when deciding on the limits of genera, for which reason the Vanda tribe has many genera and the Dendrobium tribe few. But it is fairly clear that some sections of Dendrobium are no more nearly related than some genera of the Vanda tribe; species of one section will often not cross with species of another, though intergeneric crosses in the Vanda tribe are common.

Cytological evidences support Holttum's views (Tanaka and Kamemoto, 1960, 1961; Kamemoto and Shindo, 1962; Shindo and Kamemoto, in press). The divergence between sections of *Dendrobium* as measured by the degree of chromosomal homology is often much greater than that between some genera of the *Vanda* alliance. For example, chromosome homology among strap-leaved *Vanda, Neofinetia,* and *Ascocentrum* or between terete-leaved *Vanda* and *Luisia* is much stronger than that among some sections of the *Dendrobium* genus. From the cytological standpoint, the entire *Dendrobium* genus with its 30 or more sections is somewhat comparable to the entire *Vanda* alliance comprising numerous genera and therefore, if taxonomy of these groups were to be based on chromosome homology, the merger of several genera in the *Vanda* alliance and the elevation of several sections of the *Dendrobium* genus to generic rank are indicated.

Dressler and Dodson (1960) have concluded that there are no infallible "key characters" universally applicable for orchid classification. Emphasis on a single or limited number of taxonomic characters will inevitably lead to over-splitting or over-lumping, since different groups of orchids may have different rates of divergence of certain characters. It appears that for both *Dendrobium* and *Vanda* alliances, major revisions in classification based on an intensive study of morphological characters coupled with the accumulated knowledge on crossability and chromosome homology is highly desirable.

SUMMARY

Meiotic chromosome behavior was observed for species and intra- and intersectional hybrids involving Ceratobium, Phalaenanthe, and Latourea of the genus *Dendrobium.* Meiosis was regular in all species, showing 19 bivalents at metaphase I. The within-section diploid hybrids of Ceratobium formed 19 bivalents as in the

TABLE 9

SPORAD FORMATION IN BETWEEN-SECTION HYBRIDS

SECTION	HYBRID	SPORAD						TOTAL
		Tetrad	Tetrad+ms*	Triad	Dyad	Dyad+ms*	Monad	
Phalaenanthe x Ceratobium	*D. phalaenopsis* x *D. undulatum*	95	1		1	3		100
	D. phalaenopsis x *D. gouldii*, #2	64	4		30	2		100
	D. phalaenopsis x *D. tokai*	94	3		3			100
	D. phalaenopsis x *D. taurinum*	95	4		1			100
	D. phalaenopsis x *D. Johannis*	92	8					100
	D. phalaenopsis x *D. veratrifolium*	87	6	1	6			100
Phalaenanthe x Latourea	*D. phalaenopsis* x *D.* New Guinea	17	2	6	56	9	10	100
Ceratobium x Latourea	*D. lasianthera* x *D. macrophyllum*	6	2	10	64	18		100

* ms = microcytes.

species, but a few heteromorphic pairs were observed in some of the hybrids, which suggested morphological changes in certain homologous chromosomes of the parental species involved.

Including the natural hybrid, *D. superbiens,* the between-section diploid hybrids of Phalaenanthe and Ceratobium exhibited irregularities in meiosis with the number of bivalents in each hybrid averaging from 15.7 to 18.9.

A within-Ceratobium tetraploid hybrid, *D. stratiotes* x *D. undulatum* formed 1 or 2 quadrivalents and behaved somewhat like an autotetraploid, while a tetraploid hybrid between Ceratobium and Phalaenanthe, *D. phalaenopsis* x *D. gouldii* formed only bivalents, similar to an amphidiploid.

A Ceratobium-Latourea hybrid formed an average of 10.8 bivalents per PMC, while a Phalaenanthe-Latourea hybrid formed only 1.8 bivalents. It can be concluded that Ceratobium and Phalaenanthe are relatively closely related, while Latourea is more distantly related to Ceratobium and Phalaenanthe, and that if sequential divergence occurred in these groups, the order appears to be Latourea to Ceratobium to Phalaenanthe.

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