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Cytogenetics and cytotaxonomy of some Brazilian species of Cymbidioid orchids

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Abstract

The Cymbidioid phylad presents the widest chromosome number variation among orchids, with records varying from 2n = 10 in *Psygmorchis pusilla* to 2n = 168 in two species of *Oncidium*. In the present work, a total of 44 species were studied belonging to 20 Cymbidioid genera, as a contribution to clarifying the karyological evolution of the group. All the plants investigated were collected in Brazil, mainly in the northeast region. The chromosome variation found was similar to that previously registered in the literature. Chromosome numbers observed were: 2n = 54 (subtribe Eulophiinae), 2n = 44, 46, 92 (subtribe Cyrtopodiinae), 2n = 54, ca. 108 (subtribe Catasetinae), 2n = 52, ca. 96 (subtribe Zygopetalinae), 2n = 40, 80 (subtribe Lycastinae), 2n = 40, 42 (subtribe Maxillariinae), 2n = 40 (subtribe Stanhopeinae), 2n = 56 (subtribe Ornithocephalinae), and 2n = 12, 20, 30, 36, 42, 44, 56, 112, ca. 168 (subtribe Oncidiinae). Interphase nuclei varied widely from simple chromocenter to complex chromocenter types, with no apparent cytotaxonomic value. In the genera *Catasetum* and *Oncidium*, the terrestrial and lithophytic species presented higher ploidy levels than the epiphytic species, suggesting a higher adaptability of the polyploids to those habitats. The primary base number x = 7 seems to be associated to the haploid chromosome numbers of most Cymbidioid groups, although n = 7 was observed only in two extant genera of Oncidiinae. For each tribe, subtribe and genus the probable base numbers were discussed along with the possible relationships to the primary base number $x_1 = 7$ admitted for the whole phylad.

INTRODUCTION

The Cymbidioid phylad (*sensu* Dressler, 1993) consists mainly of pantropical epiphytic species, with approximately 275 genera and 4300 species, including 86 genera and 654 species throughout Brazil (Pabst and Dungs, 1977). The phylad is formed basically by the ancient subfamily Vandoideae (*sensu* Dressler, 1981), excluding the tribes Polystachieae and Vandeae, and is characterized by having two polinia whose texture varies from firm to hard (Dressler, 1993). It is a morphologically variable group, including ornamental species, mainly in the subtribes Cyrtopodiinae (*Cymbidium*) and Oncidiinae (*Odontoglossum*, *Miltonia* and *Oncidium*), which have been more widely studied cytologically (see, e.g., Sinotô, 1962; Charanasri *et al*., 1973).

Cymbidioid phylad has the highest variation in chromosome number of all orchids: 2n = 10 in *Psygmorchis pusilla* (Dodson, 1957a,b) to 2n = 168 in a horticultural variety of *Oncidium varicosum* (Sinotô, 1962). There are previous reports for approximately 495 species distributed throughout 60 genera, of which 47 species belonging to 39 genera are from Brazil, representing 9.93% of all species analyzed. *Oncidium*, *Catasetum*, *Stanhopea*, *Brassia*, *Miltonia*, and *Zygopetalum* are the best studied of these genera (Blumenschein, 1960a). Chromosome number variation in Cymbidioid phylad and orchids as a whole is intriguing because most of the genera have high ploidy levels and variable base numbers (Goldblatt, 1980; Ehrendorfer, 1980). The base number of the family is still uncertain, difficulting to estimate species ploidy level and to understand the karyological evolution of the family. Raven (1975) reviewed the angiosperm's base number and considered it premature to suggest a base number for Orchidaceae.

In the present study, chromosome number and interphase nuclear types were investigated relative to 44 species of 20 genera of Cymbidioid orchids occurring in Brazil. Besides, the variability in chromosome number within the phylad was reviewed, along with its compatibility with the taxonomic treatment proposed by Dressler (1993), and the most probable base number for each genus, subtribe and tribe of the group.

MATERIAL AND METHODS

All species analyzed in the present work were collected on excursions throughout Brazil, especially in northeast region. The material was cultivated in the greenhouse of the Universidade Federal Rural de Pernambuco and in the experimental garden of the Department of Botany at the Universidade Federal de Pernambuco. Vouchers were deposited in EAN, JPB, PEUFR, HST and UFP Herbaria (acronyms in agreement with Mori *et al*., 1989). For each species, whenever possible, a minimum of three individuals and more than one population were analyzed (Table I). The identifications were based on Cogniaux (1906), Hoehne (1942, 1953) and Pabst and Dungs (1975, 1977) and, in some cases, submitted and identified by specialists.

Mitotic analyses were undertaken mainly on root tips or ovary walls pretreated with 0.002 M 8-hydroxyquinoline at 4°C for 24 h. Root tips and young flower buds (for mitotic or meiotic analysis) were fixed in Carnoy 3:1 (ethanol/acetic acid) for a period varying from 3 to 24 h and later stored at -20ºC in the same solution. For slide preparation, the material was hydrolyzed in 5 N HCl for 20-30 min at room temperature and stained with Giemsa 2% (Guerra, 1983) or hematoxylin at 1% (Guerra, 1999). Photomicrographs were taken with Kodak Imagelink or Agfa Copex Pan films, using a Leica DMRB photomicroscope adjusted to 25 ASA.

RESULTS AND DISCUSSION

Karyological variation

A total of 44 species belonging to 20 genera and two of the four tribes from Cymbidioid phylad were analyzed (Table I). Chromosome numbers varied from 2n = 12 in *Psygmorchis pusilla* to 2n = ca. 168 in *Oncidium* aff. *flexuosum*. No interpopulational numeric variation was observed in species with more than one population analyzed (*Bifrenaria magnicalcarata*, *Catasetum discolor*, *Cyrtopodium intermedium*, *C. paranaense*, *Notylia lyrata*, *Oncidium barbatum*, *O. cebolleta*, *Psygmorchis pusilla*, *Rodriguezia bahiensis* and *Trichocentrum cornucopiae*). In *Oeceoclades maculata*, samples of four populations produced clumped cells with 2n = ca. 52, but in other three populations, in which the best metaphase was obtained, 2n = 54 was always observed (Figure 1a), suggesting that they have the same number.

Figures 1 to 5 illustrate the karyotype of all species analyzed. Chromosome morphology, whenever observed, was very variable, with metacentric, submetacentric and acrocentric chromosomes in almost all species. Satellites were observed in a few species, and up to two satellites were found in *Catasetum barbatum*, *Coryanthes speciosa*, *Trichocentrum cornucopiae*, *Oncidium pumillum* and *Notylia lyrata*.

The interphase nuclei varied from the simple to complex chromocenter types, according to the classification of Tanaka (1971). In *Dichaea panamensis*, *Catasetum barbatum*, *C. discolor*, *C. luridum*, *Dipteranthus duchii*, *Dipteranthus* sp., *Cyrtopodium blanchetii*, *Gongora quinquenervis*, *Oeceoclades maculata*, *Trigonidium acuminatum* and *T. obtusum*, along with all the species of

Table I - List of species analyzed with respective chromosome numbers (n and/or 2n), provenances, habitats, numbers of collector and herbarium where each material is deposited.

Species	n	2n	Provenance	Habitat	Collector (No.)	Herbarium
TRIBE CYMBIDIEAE						
Subtribe Eulophiinae						
Oeceoclades maculata (Lindl.) Lindl.		ca. 52	Sete Cidades, PI	Terrestrial	L.P. Felix *et al.*, S/N	HST
		ca. 52	Maranguape, CE	Terrestrial	L.P. Felix, S/N	HST
		ca. 52	Bezerros, PE	Terrestrial	L.P. Felix, 8916	HST
		ca. 52	Rio de Contas, BA	Terrestrial	L.P. Felix, 8677	PEUFR
		54	Goiana, PE	Terrestrial	L.P. Felix, S/N	PEUFR
		54	Cabo, PE	Terrestrial	L.P. Felix, 8956	PEUFR
		54	Recife, PE	Terrestrial	L.P. Felix, 9378	PEUFR
Subtribe Cyrtopodiinae						
Cyrtopodium blanchetii Rchb. f.		92	Santa Rita, PB	Terrestrial	L.P. Felix, S/N	JPB
C. gigas (Vell.) Hoehne		46	Juazeiro, BA	Epiphytic	L.P. Felix, 8541	EAN
C. inaldianum L.C. Menezes		46	Conde, PB	Terrestrial	L.P. Felix, S/N	EAN
C. intermedium Brade		46	Bezerros, PE	Terrestrial	L.P. Felix, 8990	PEUFR
	23		Camocim do São Félix, PE	Terrestrial	L.P. Felix, 9370	PEUFR
C. paranaense Schltr.		46	Bezerros, PE	Terrestrial/Lithophytic	L.P. Felix, 7692	PEUFR
		46	São Lourenço da Mata, PE	Terrestrial	J. Alves, S/N	UFP
Cyrtopodium eugenii Rchb. f.	22		Ibicoara, BA	Terrestrial	L.P. Felix, 8797	HST
Subtribe Catasetinae						
Catasetum barbatum Lindl.		54	União, PI	Epiphytic	L.P. Felix *et al.*, 9043	HST
C. luridum (Link) Lindl.		54	José de Freitas, PI	Epiphytic	L.P. Felix, 9042	HST
C. discolor Lindl.		ca. 108	Camocim do São Félix, PE	Terrestrial/Lithophytic	L.P. Felix, 9047	EAN
		ca. 108	Bonito, PE	Terrestrial/Lithophytic	L.P. Felix, 8379	HST
C. macrocarpum Rich.		54	Cabo, PE	Epiphytic	L.P. Felix, 9393	HST
C. purum Nees e Sinnings		54	Carmópolis, SE	Epiphytic	L.P. Felix, 8818	PEUFR
TRIBE MAXILLARIEAE						
Subtribe Zygopetalinae						
Dichaea panamensis Lindl.		52	Cabo, PE	Epiphytic	L.P. Felix, 8380	HST
Koelensteinia tricolor (Lindl.) Rchb. f.		ca. 96	Ouro Preto, MG	Terrestrial	L.P. Felix, 9331	PEUFR
Subtribe Lycastinae						
Bifrenaria magnicalcarata (Hoehne) Pabst		80	Morro do Chapéu, BA	Lithophytic	L.P. Felix, 8627	PEUFR
		80	Rio de Contas, BA	Lithophytic	L.P. Felix, 8837	PEUFR
Xylobium foveatum (Lindl.) Nichols		40	Santa Teresinha, BA	Epiphytic	L.P. Felix, 8856	HST

Continued on the next page

Table I - Continued

Species	n	2n	Provenance	Habitat	Collector (No.)	Herbarium
Subtribe Maxillariinae						
Maxillaria discolor (Lodd. ex Lindl.) Rchb. f.		42	Belo Jardim, PE	Epiphytic	L.P. Felix, 9052	EAN
M. rufescens Lindl.		40	Domingos Martins, ES	Epiphytic	L.P. Felix, 9361	PEUFR
Trigonidium acuminatum Batem. ex Lindl.		40	Esperança, PB	Lithophytic	L.P. Felix, 9377	
T. obtusum Lindl.		40	Belo Jardim, PE	Epiphytic	L.P. Felix, 9053	EAN
Subtribe Stanhopeinae						
Coryanthes speciosa Hook.		40	Maceió, Al	Epiphytic	L.P. Felix, 9389	PEUFR
Gongora quinquenervis Ruiz & Pavon		40	Belo Jardim, PE	Epiphytic	L.P. Felix, 8298	HST
Subtribe Ornithocephalinae						
Dipteranthus duchii Pabst		ca. 56	Bonito, PE	Epiphytic	L.P. Felix, 8948	EAN
Dipeteranthus sp.		56	Areia, PB	Epiphytic	L.P. Felix, 9055	EAN
Subtribe Oncidiinae						
Brassia lawrenciana Lindl.		60	Recife, PE	Cultivated	L.P. Felix, 9395	PEUFR
Lockartia goyazensis Rchb. f.		56	Piracanjuba, GO	Epiphytic	L.P. Felix, 9376	PEUFR
		56	Foz do Iguaçu, PR	Cultivated	M. Guerra, S/N	PEUFR
Miltonia flavescens Lindl.		60	Rio de Janeiro, RJ	Epiphytic	L.P. Felix, 9394	PEUFR
Notylia lyrata S.P. Moore		ca. 44	Areia, PB	Epiphytic	L.P. Felix, 9045	EAN
		44	Morro do Chapéu, BA	Epiphytic	L.P. Felix, 8679	PEUFR
Oncidium barbatum Lindl.		56	São Lourenço da Mata, PE	Epiphytic	L.P. Felix, 9046	HST
		56	Morro do Chapéu, BA	Epiphytic	L.P. Felix, S/N	PEUFR
		56	Garanhuns, PE	Epiphytic	L.P. Felix, 8905	PEUFR
O. baueri Lindl.		56	Recife, PE	Epiphytic	K. Santos, S/N	PEUFR
O. blanchetii Rchb. f.		ca. 112	Morro do Chapéu, BA	Terrestrial	L.P. Felix, 8594	HST
O. cebolleta Sw.		36	Areia, PB	Epiphytic	L.P. Felix, S/N	EAN
		36	Gravatá, PE	Epiphytic	L.P. Felix, 8937	EAN
O. aff. *Crispum* Lodd.		56	Domingos Martins, RS	Epiphytic	L.P. Felix, 9350	PEUFR
O. flexuosum Sims.	28		Rio Grande, RS	Epiphytic	L.P. Felix, 8974	HST
O. aff. *flexuosum* Sims.		ca. 168	São Caetano, PE	Lithophytic	L.P. Felix, 8305	HST
O. gravesianum Rolfe		56	Morro do Chapéu, BA	Epiphytic	L.P. Felix, 8629	EAN
O. loefgrenii Cogn.	28	56	Morro do Chapéu, BA	Epiphytic	L.P. Felix, 8929	HST
O. pumillum Lindl.		30	Rio Grande, RS	Epiphytic	L.P. Felix, 8975	HST
O. varicosum Lindl.	56	112	Morro do Chapéu, BA	Epiphytic/Terrestrial	L.P. Felix, 8657	PEUFR
Oncidium paranaense Krzl.		56	Piratini, RS	Epiphytic	L.P. Felix, 8967	PEUFR
Psygmorchis pusilla (L.) Dodson & Dressler	6	12	Camocim do São Félix, PE	Epiphytic	L.P. Felix, 9048	HST
	6	12	Belém do Pará, PA	Epiphytic	L.P. Felix, 9413	PEUFR
Rodriguezia bahiensis Rchb. f.		ca. 42	Recife, PE	Epiphytic	L.P. Felix, 9049	HST
		42	Maranguape, CE	Epiphytic	L.P. Felix, 8269	EAN
R. lanceolata Ruiz & Pavon		42	Acará, PA	Epiphytic	L.P. Felix, 9050	EAN
Trichocentrum cornucopiae Lindl. & Rchb. f.		20	Carmópolis, SE	Epiphytic	L.P. Felix, 9391	HST
		20	Canavieiras, BA	Epiphytic	L.P. Felix, 8951	HST

AL, Alagoas; BA, Bahia; CE, Ceará; GO, Goiás; MA, Maranhão; MG, Minas Gerais; PA, Pará; PB, Paraíba; PE, Pernambuco; PI, Piauí; RN, Rio Grande do Norte; RS, Rio Grande do Sul; SE, Sergipe.

Oncidiinae (except *Brassia lawrenciana*), interphase nuclei of simple chromocenter type were observed, with small heteropycnotic blocks and fibrous diffuse chromatin. Intermediate nuclei between simple and complex chromocenter types were observed in *Cyrtopodium gigas*, *C. inaldianum*, *C. intermedium*, *C. paranaense*, *C. eugenii*, *Catasetum macrocarpum*, *C. purum* and *Brassia lawrenciana*. These nuclei were characterized by the presence of several partially aggregate heteropycnotic blocks and irregular outline which were gradually transformed into diffuse chromatin. Interphase nuclei of the complex chromocenter type, with large, strongly stained heteropycnotic blocks, were found in *Koelensteinia tricolor*, *Maxillaria discolor*, *M. rufescens*, *Coryanthes speciosa* and *Xylobium foveatum*.

In some other families, analysis of the chromatin organization in interphase nuclei has contributed to an understanding of the genomic diversification, independent of number and chromosome morphology (Morawetz, 1986; Röser, 1994). There is a general tendency toward the conservation of a single interphase nuclear type throughout a genus or a higher taxonomic category, as in Rutaceae, subfamily Aurantioideae (Guerra, 1987). In orchids, Tanaka (1971) described five different types of interphase nuclei based on observations in 115 species of 52 genera. However, the occurrence of more than one interphase nuclear type in a single genus has been described, as in *Habenaria* (Félix and Guerra, 1998) and *Platanthera* (Yokota, 1990). In *Catasetum* and *Cyrtopodium*, which present chromosome numbers and morphology relatively constant, two different types of interphase nuclei occur. Otherwise, the occurrence of simple chromocenter nuclei in nearly all Oncidiinae species seems to reflect the uniformity of this

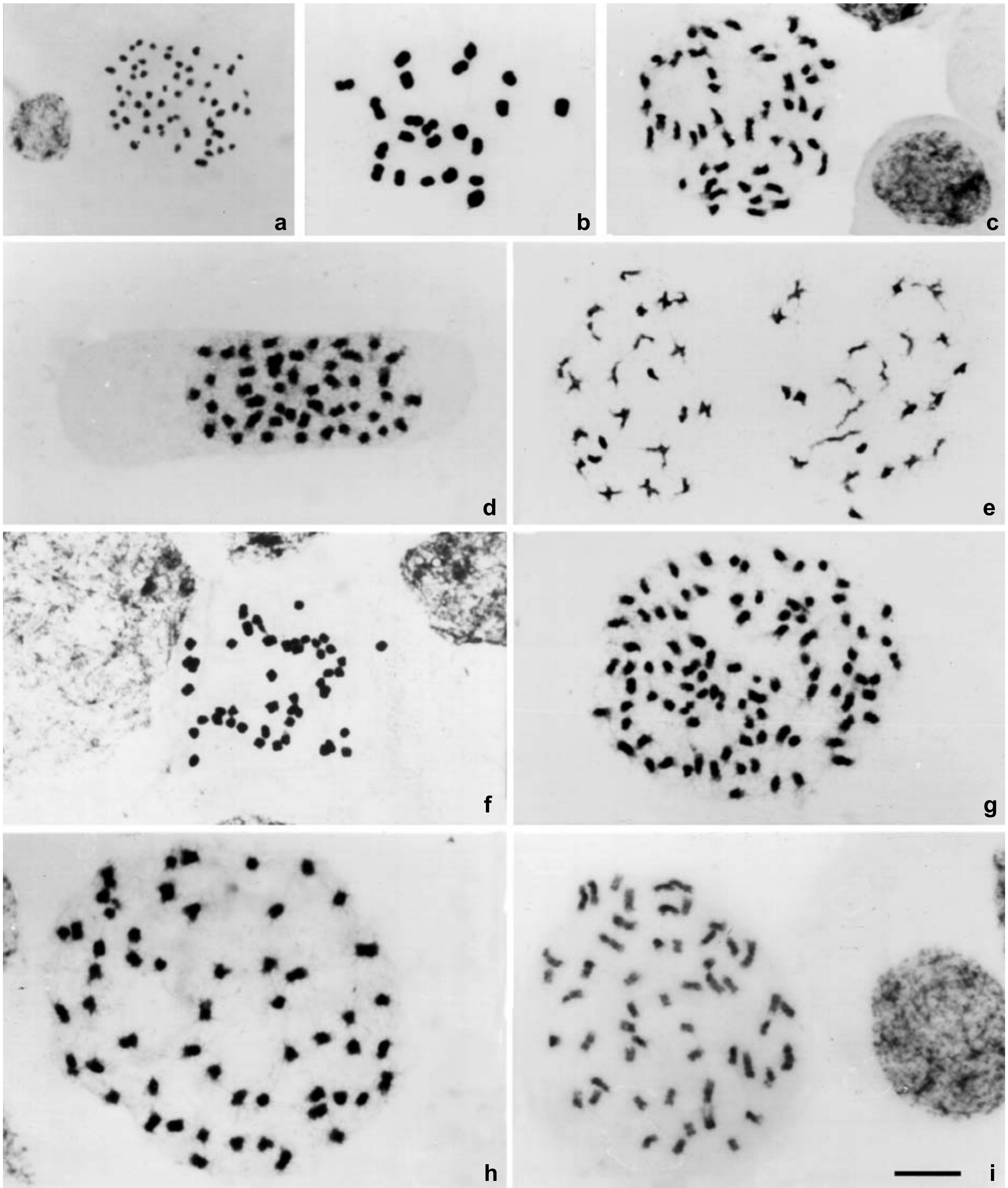

Figure 1 - Chromosome complements and interphase nuclei of orchid species of the subtribes Eulophiinae, Cyrtopodiineae and Catasetinae. (**a**) *Oeceoclades maculata* (2n = ca. 52) with two larger chromosome (bottom); (**b**) diakinesis of *Cyrtopodium eugenii* with 22 bivalents; (**c**) *C. gigas* (2n = 46); (**d**) *C. inaldianum* (2n = 46); (**e**) two cells in prophase II of *C. intermedium* (n = 23); (**f**) *C. paranaense* (2n = 46); (**g**) *C. blanchetii* (2n = 92); (**h**) *Catasetum barbatum* (n = 54), and (**i**) *C. luridum* (2n = 54). Bar represents 10 µm.

group (Chase, 1986). Therefore, the meaning of this variation in orchids needs to be better understood.

The chromosome number variation of Cymbidioid seems to be much more elucidative. In order to attempt to understand the chromosome numeric variation of the phylad, a complete review of the recorded chromosome numbers was made, based on the review of Tanaka and Kamemoto (1984), followed by the chromosome number indexes published by Fedorov (1969), Moore (1973, 1974, 1977), Goldblatt (1984, 1985, 1988) and Goldblatt and Johnson (1990, 1991, 1994, 1996). Furthermore, the chromosome numbers were checked in many original papers, although it

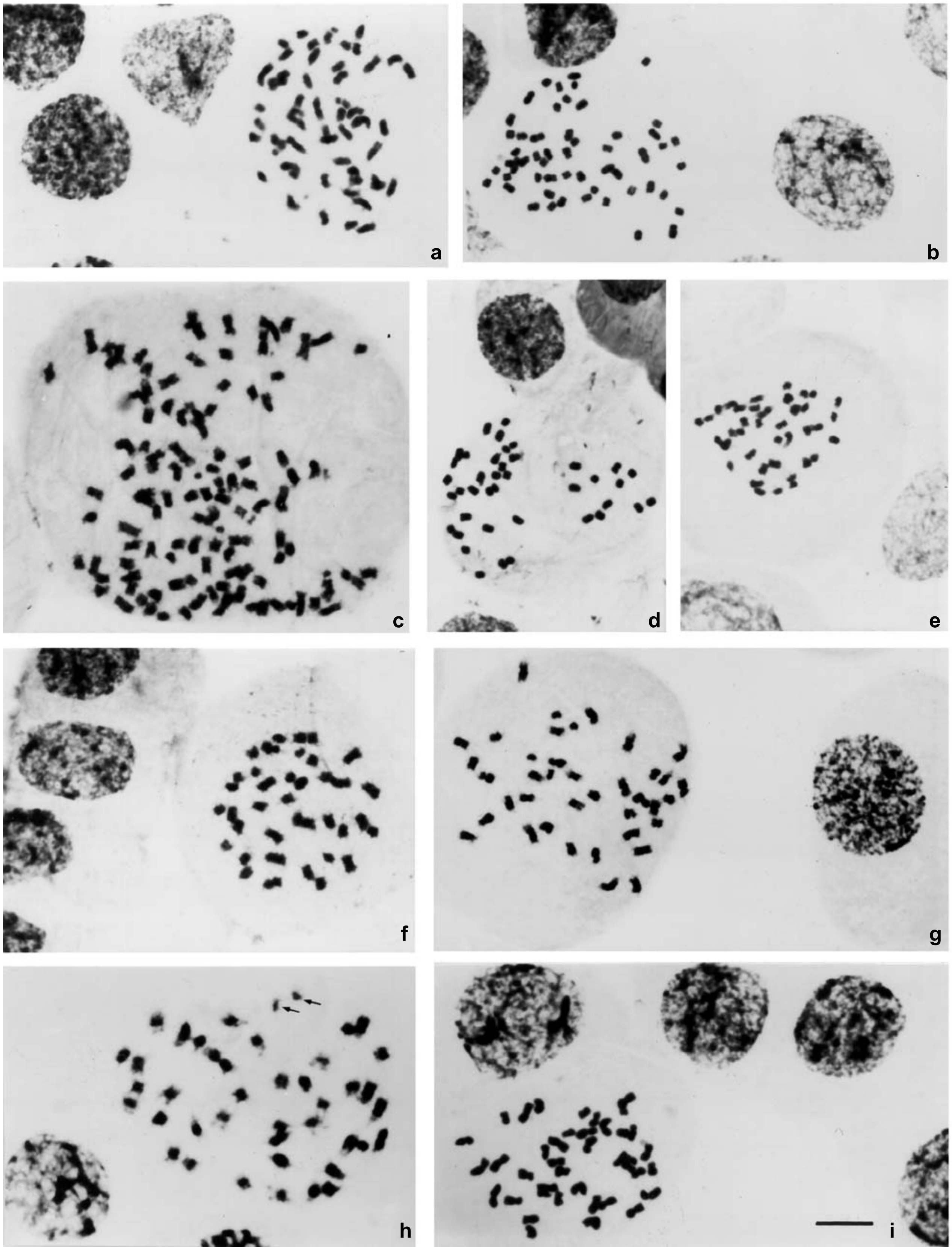

Figure 2 - Chromosome complements and interphase nuclei of orchid species of the subtribes Catasetinae, Maxillariinae, Stanhopeinae and Lycastinae. (**a**) *Catasetum macrocarpum* (2n = 54); (**b**) *C. purum* (2n = 54); (**c**) *C. discolor* (2n = ca. 108); (**d**) *Maxillaria rufescens* (2n = 40); (**e**) *Trigonidium acuminatum* (2n = 40); (**f**) *T. obtusum* (2n = 40); (**g**) *Gongora quinquenervis* (2n = 40); (**h**) *Coryanthes speciosa* (2n = 40) (arrows indicate detached satellites), and (**i**) *Xylobium foveatum* (2n = 40). Bar represents 10 µm.

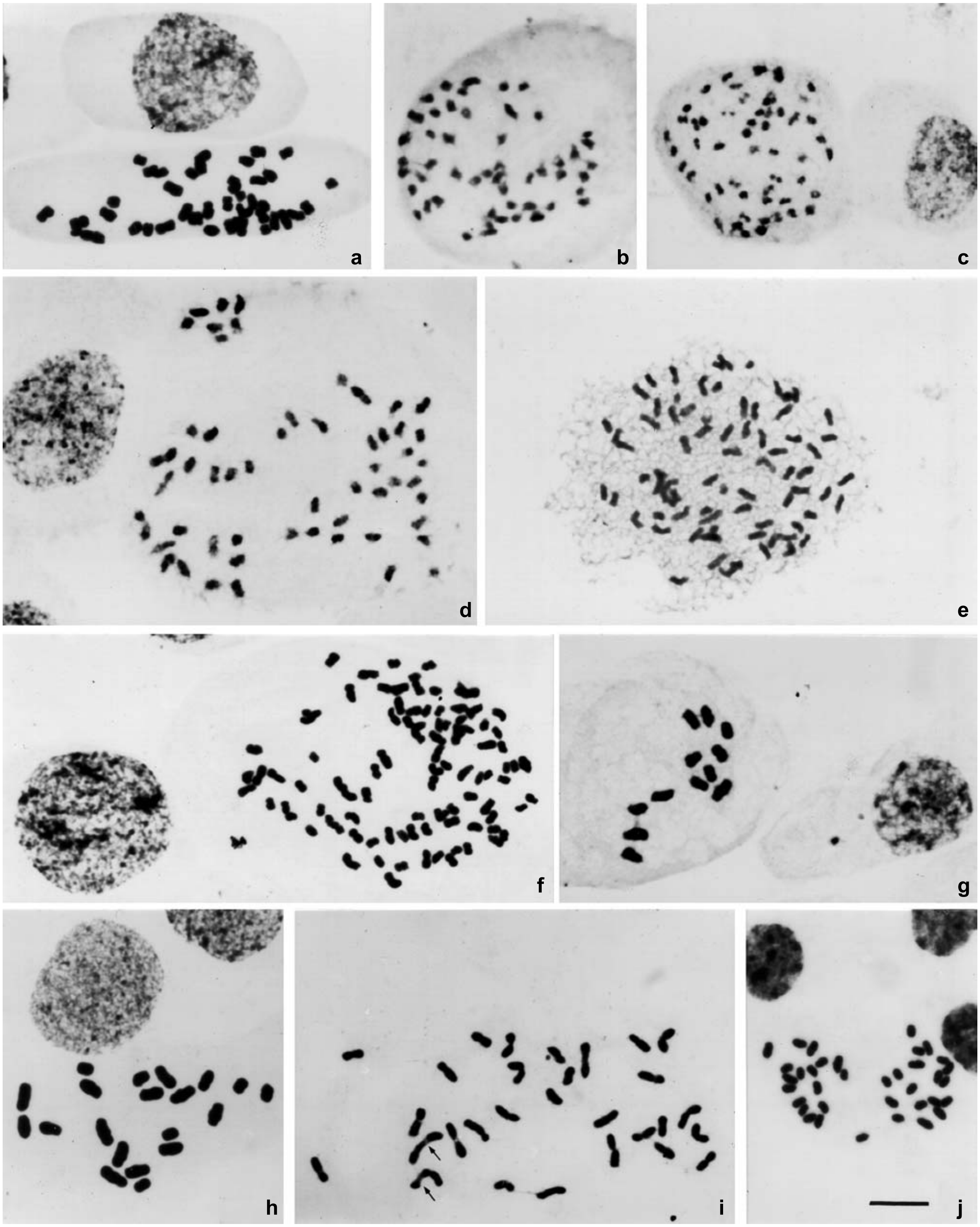

Figure 3 - Chromosome complements and interphase nuclei of orchid species of the subtribes Maxillariinae, Zygopetalinae, Lycastinae and Oncidiinae: (**a**) *Maxillaria discolor* (2n = 42); (**b**) *Dichaea panamensis* (2n = 52); (**c**) *Dipteranthus duchii* (2n = ca. 56); (**d**) *Dipteranthus* sp. (2n = 56); (**e**) *Bifrenaria magnicalcarata* (2n = 80); (**f**) *Koelensteinia tricolor* (2n = ca. 96); (**g**) *Psygmorchis pusilla* (2n = 12); (**h**) *Trichocentrum cornucopiae* (2n = 20); (**i**) *Oncidium pumillum* (2n = 30) (arrows indicate secondary constriction), and (**j**) *O. cebolleta* (2n = 36). Bar represents 10 µm.

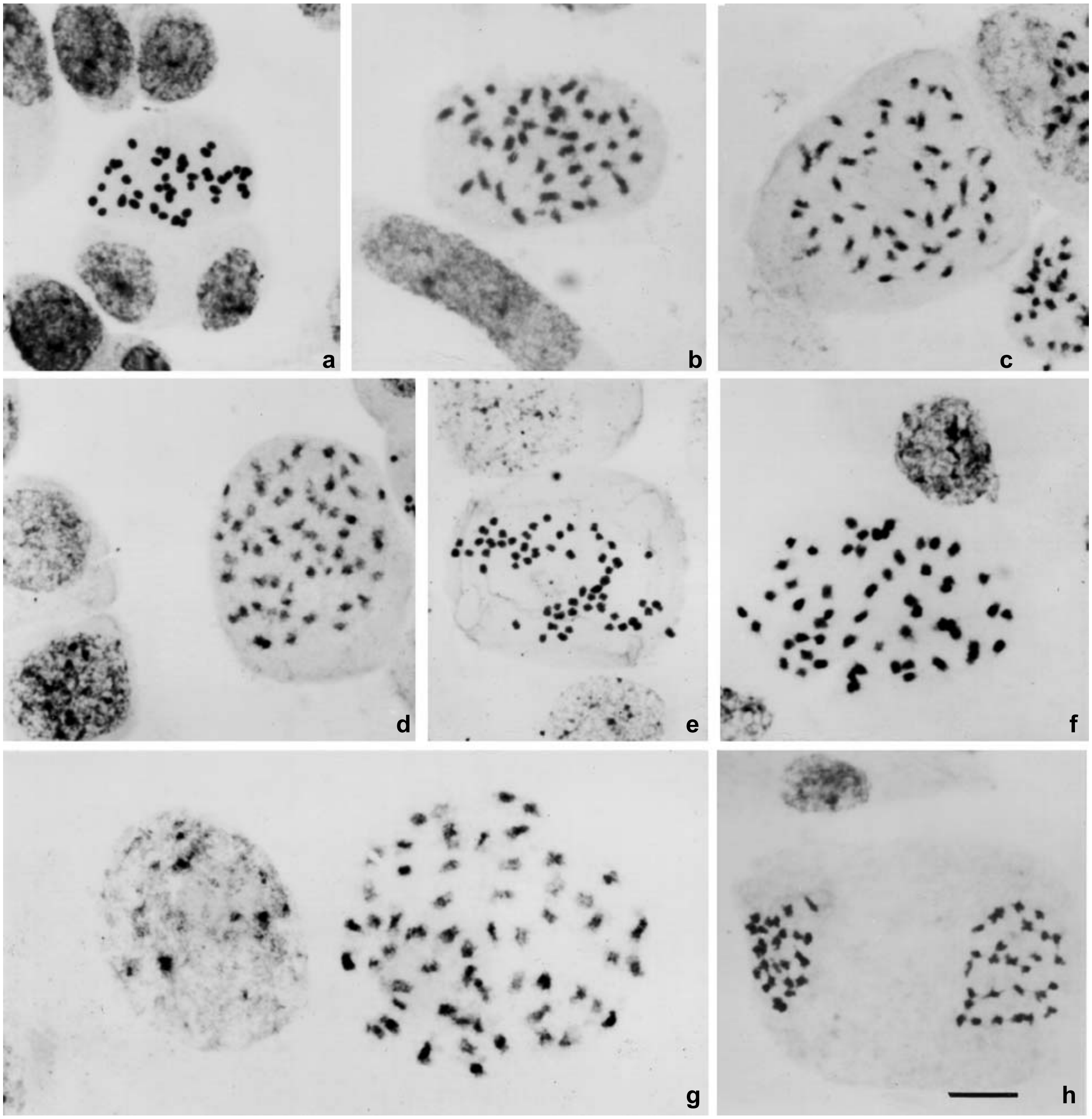

Figure 4 - Chromosome complements and interphase nuclei of orchid species of the subtribe Oncidiinae: (**a**) mitotic metaphase and interphase nucleus of *Rodriguezia bahiensis* (2n = 42); (**b**) *R. lanceolata* (2n = 42); (**c**) *Notylia lyrata* (2n = 44); (**d**) *Lockartia goyazensis* (2n = 56), and (**e**) *Oncidium barbatum* (2n = 56); (**f**) *O. baueri* (2n = 56); (**g**) *O.* aff. *crispum* (2n = 56), and (**h**) meiotic prophase II of *O. flexuosum* (n = 28). Bar represents 10 µm.

has not been possible to obtain copies of all of them, since some journals were very difficult to access.

Table II presents the complete list of cytologically known Cymbidioid species, including original data of the present work. These data are synthesized in Table III, which shows the chromosome numbers recorded within each genus in decreasing order of frequency. The most probable base number of each genus was also tentatively recognized. The base number was identified as one of the haploid number actually found in the genus that most parsimoniously explains the chromosome number variation found in the taxon and more related genera (Guerra, 2000). Based on this concept, it was possible to indicate the number that most probably represents the original haploid complement for each genus. The criterion of the "most frequent" chromosome number was accepted as an indicator of the base number only when it was well represented in the related genera. In many genera, such as *Liparis*, *Eulophia* and *Odontoglossum*, two or more numbers seemed equally probable and were provisorily maintained as base numbers, although only one of them should represent the primary base number of each genus.

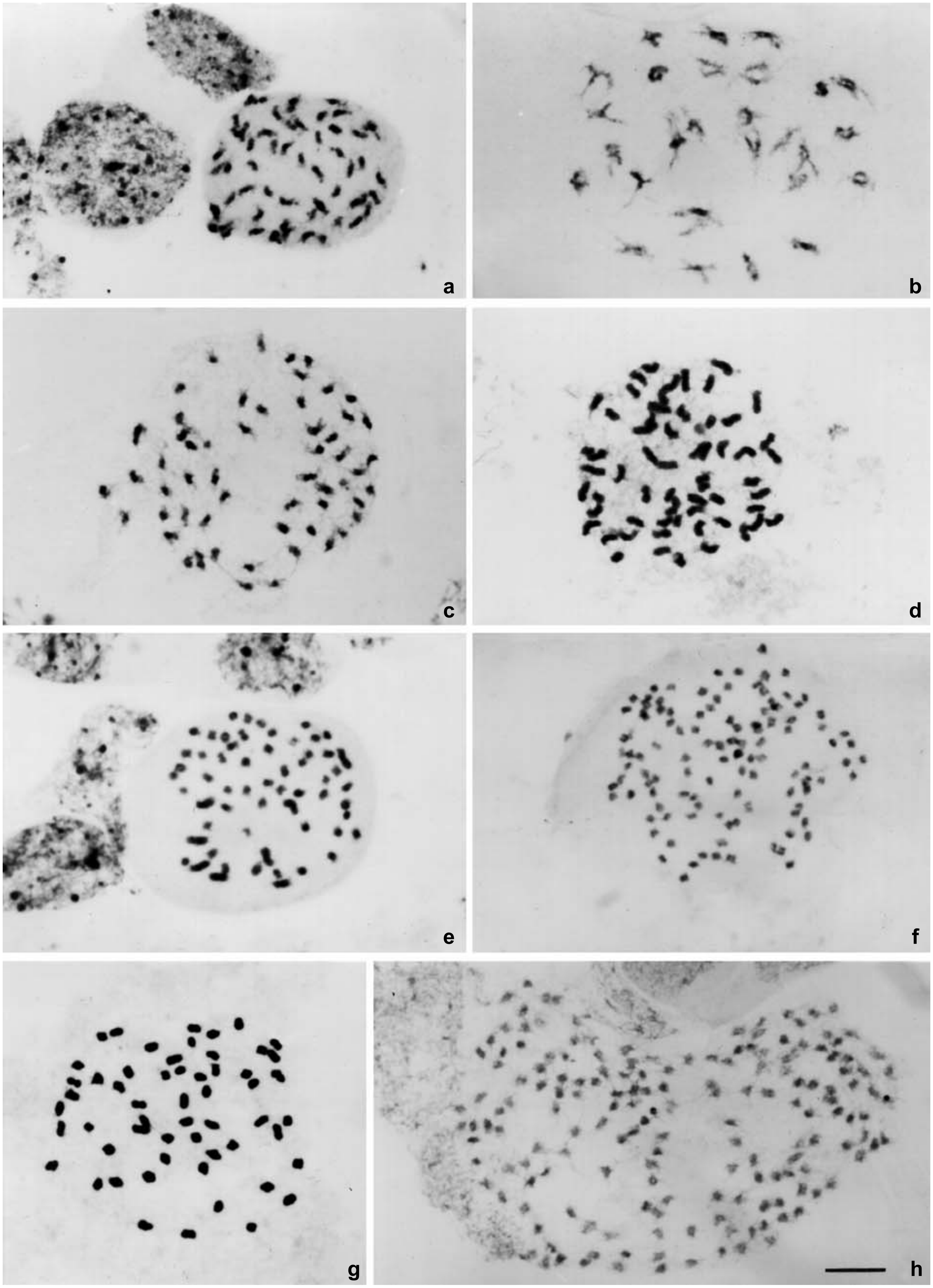

Figure 5 - Chromosome complements and interphase nuclei of Brazilian species of Oncidiinae: (**a**) *Oncidium gravesianum* (2n = 56); (**b**) diplotene of *O. loefgrenii* (n = 28^{II}); (**c**) *Oncidium paranaense* (2n = 56); (**d**) *Brassia lawrenciana* (2n = 60); (**e**) *Miltonia flavescens* (2n = 60). Observe eight larger chromosomes; (**f**) diakinesis of *Oncidium varicosum* (n = 56^{II}); (**g**) *O. blanchetii* (2n = ca. 112), and (**h**) *O.* aff. *flexuosum* (2n = ca. 168). Bar represents 10 μm.

Table II - Chromosome numbers in Cymbidioid (organized according to Dressler, 1993).

Taxon	n	2n	Sources
TRIBE MALAXIDEAE			
Liparis amesiana Schltr.		30	TK84
L. bautingensis Tang & Wang		38	GJ91, GJ96
L. bituberculata Lindl.		42	G84
L. bootanensis Griffith	19		M77
		38	G88, GJ91, GJ96
L. caespitosa Lindl.		40	G88
L. confusa F.F. Sm.		30	TK84
L. cordifolia Hook. f.	10		TK84, G88, GJ94
L. deflexa Hook. f.	21		TK84, G88, GJ94
L. dunnii Rolfe		20	G88
L. duthiei Hook.	15		M73
L. elegans Lindl.		30	G85
L. elongata		30	G85
L. epiphytica Schltr.		42	G84
L. ferruginea Lindl.		42	TK84
L. fimbriata Kerr		42	TK84
L. formosa		42	M73
L. formosa var. *hachijoensis*		42	M73
L. fugisanensis F. Mackawa		30	GJ91
L. ganblei Hook. f.	18		M73
L. glossula Reichb.	10		M73, TK84, G88, GJ94
L. guineense Lindl.		42	G84
L. inconspicua Hook.	19		G84
L. japonica (Miq.) Maxim.		30	TK84, GJ91
L. keitaoensis Hay		30	M74
L. krameri Franc. & Savat.		30	TK84, GJ91
L. kumokiri F. Mack.		30	M73
	13		TK84
		26, 30	GJ91
L. kuramari		30	M73
L. loeseli (L.) Rich.		32	TK84
L. longipes Lindl.		42	M73
		38	G84
		22 + 6b	GJ90
L. longipes var. *spathulata* Rodley	15		M73
L. luteola Lindl.	19		TK84
L. mannii Rchb. f.		38	G88
L. makinoana Schltr.		30	TK84, GJ91
L. nepalensis Lindl.	18		M73
L. nervosa (Sw.) Lindl.	21	42	TK84
		42	TK84, G84
L. paradoxa Rchb. f.	21		TK84, G84, G88, GJ94
L. perpusilla Hook. f.	15		M73
L. plantaginea Lindl.	19		TK84

Continued

Table II - Continued

Taxon	n	2n	Sources
Liparis plicata Franch. & Savat.		42	TK84
		38	M73
L. prazeri King & Pantl.		42	G84
L. pulchella Hook. f.	15		M77
L. pulcherrima		68-80	F69
L. pulverulenta Guillaumin	40		TK84
L. pusilla Ridl.		40	M73
L. ressupinata Ridl.	14		M73
	28		M77
L. rostrata L.	14	28	TK84, G88, GJ90, GJ94
L. siamensis Rolfe		ca. 42	TK84
L. stricklandiana (Thumb.) Lindl.		76	GJ91
L. taiwaniana Hayata		38	TK84
L. viridiflora Blume	15		TK84, G84
Liparis sp.		38, 42	G84
Liparis sp.		38	GJ91
Liparis sp.		38	GJ96
Liparis sp.		38	GJ96
Malaxis acuminata D. Don.	21		G84, G88, GJ94
M. boninensis (Koidz.) C. Nackej.		36	TK84
M. cylindrostachya (Lindl.) Kuntze	15 + 0 - 2b		G88
M. densiflora Kuntze		42	G84
		60	G85
M. latifolia Sm. ex Rees	21		G84, G88
		42	GJ91, GJ96
M. monophylla (L.) Sw.	15	30	TK84, G85
M. monophylla subsp. *brachypoda* (Gray) Love & Love		28	TK84, G84
		30	G88
M. muscifera (Lindl.) Kuntze	30		TK84, G88, GJ94
M. orbicularis (Smith & Jeff.) Tang & Wang		ca. 40	TK84
M. paludosa (L.) Sw.	14	28	M73
M. parviflora Blume		44	M73
M. siamensis (Rolfe & Dow.) Seid. & Smit.		ca. 42	TK84
M. versicolor Sant. & Kap.		42	G84
M. versicolor Lindl.		60	G85
Oberonia auriculata King & Pantl.	15		TK84, G88, GJ94
O. bicornis Lindl.		30	G85
O. brachyphylla Blatt. & McCann		30	G84
O. brunoniana Wt.		30	TK84, G84, GJ90
O. caulescens Lindl.	15		G85
O. ensiformis (Sw.) Lindl.		30	TK84, G84
	15		G84, G88, GJ94
O. equitans (Forst. f.) Drake		60	G88
O. falcata King & Pantl.		30	G85

Continued on the next page

Table II - Continued

Taxon	n	2n	Sources
Oberonia falconeri Hook. f.		30	TK84
	15		TK84, G84, G88, GJ94
O. heliophyla Rchb. f.		30	G88
O. imbricata (Blume) Lindl.		30	G88
O. iridifolia (Roxb.) Lindl.	15		TK84, G88
O. iridifolia var. *denticulata* Wight		30	G84
O. integerrima Guillaumin		30	TK84
O. japonica (Maxim.) Makino		30	M73
O. longilabris King. & Pantl.		30	G85
O. mannii	15		TK84
O. micranta King. & Pantl.	15		G88
O. myriantha Lindl.	15		TK84, G84, G88, GJ94
O. obcordata Lindl.	15		M73
		30	G85
O. pachyrachis Rchb. f.	15		TK84
		30	TK84, G88, GJ94
O. parvula King & Pantl.	15		G85
O. platycaulon Wight		30	G85
O. proudlockii King & Pantl.		30	G84
O. prainiana King & Pantl.	15		M73
O. santapaui Kap.		30	TK84, G84
O. tenuis Lindl.		30	G85
O. verticilla Wight		30	TK84, G84
O. wightiana Lindl.		30	G85, GJ90
Oberonia sp.		30	GJ91
Oberonia sp.		30	GJ96
TRIBE CALYPSOEAE			
Calypso bulbosa (L.) Oakes	14	28	TK84
Corallorhiza innata R. Br.	21	42	TK84
C. maculata Raf.	42		M73
		42	G84
C. maculata subsp. *mertensiana*	20		M73
C. mertensiana Bong.	20		G85
C. striata Lindl.		42	TK84, G84
C. trifida Chatel.		42	TK84, G84, G88, GJ91
	21		TK84
Cremastra appendiculata (D. Don) Makino		48	GJ91
C. unguiculata Finet		48	TK84
C. variabilis Nakai (as *C. appendiculata*)	24	48	TK84
C. wallichiana Lindl.	26		M73
Dactylostalix ringens		42	TK84
Ephippianthus schmidtii Rchb. f.		40	TK84
		42	TK84
		36	TK84
Oreorchis indica Hook. f.	42		G88, GJ94
O. patens (Lindl.) Lindl.	24	48	M73, TK84, GJ91

Continued

Table II - Continued

Taxon	n	2n	Sources
TRIBE CYMBIDIAE			
Subtribe Eulophiinae			
Dipodium paludosum (Griff.) Rchb. f.		46	GJ91
Eulophia aculeata subsp. *huttonii*	27		M77
E. angolensis (Rchb. f.) Sum.	34, 35, 36, 37, 38		M77
E. campestris Wall.	24		G85, G88, GJ94
E. clavicornis Lindl.	50		M77
E. clavicoris var. *nutans* (Sond.) Hall	25, 47		M77
E. cristata (Sw.) Steud.		46	M73
E. ensata Lindl.	27		M77
E. euglossa (Rchb. f.) Rchb. f.		40	M73
		44	G84
E. foliosa (Lindl.) Bol.	27		M77
E. fridencii (Rchb. f.) Hall	24		M77
E. geniculata	19	38	M73
E. gracilis Lindl.	22 III	44, 66	M73
E. graminea Lindl.	27		TK84
E. guineense Lindl.		44	G84
		46	M73
		54	GJ91
E. gusukumai Masam.		56	TK84
E. hormusjii Duthie	27		M73, G84, G85, GJ94
		54	G84
E. horfallii (Batem.) Summ.		62	M73
E. leachii Gratex ex Hall	26		M77
E. leonoglossa Lindl.	27		M77
E. macowanii Rolfe	28		M77
E. macrostachya Lindl.		32	TK84
	14		G88
E. nuda Lindl.		54	M73, G84
E. nuda var. *andersonii* Hook. f.	28		G88
E. ochreata Lindl.		54	G84
E. ovalis sub. *beinensis*		42	TK84
E. ovalis sub. *ovalis* Lind.	21		M77
E. paiveana (Rchb. f.) Summerrh.	42		GJ90
E. paniculata Rolfe		60	GJ91
E. parviflora (Lindl.) Hall	25		M77
E. ramentacea Lindl.		54	TK84
E. speciosa (R. Br.) Bol.	27		M77
E. squalida Lindl.		32	TK84
E. stenophylla Summerh.	21		GJ90
E. streptopetala Lindl.	20	40	TK84
	21	42	GJ90, GJ91
E. stricta		32	TK84
E. tenella Rchb. f.	60		M77

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Table II - Continued

Taxon	n	2n	Sources
Eulophia tuberculata Bolus	50		M77
E. welwitschii (Rchb. f.) Rolfe	27		M77
E. zeyheriana Sond.	56		M77
Eulophia sp.	16	32	TK84
Eulophia sp.		82	TK84
Eulophia spp.		54, 56	G84
Oeceoclades maculata (Lindl.) Lindl.			
(as *Eulophidium maculatum* Lindl.)		54	PW
		58	G84
O. saundersiana (Rchb. f.) Garay & Taylor			
(as *Eulophidium saundrsiana* Rchb. f.)		58	M73, GJ91
Subtribe Cytopodiinae			
Anselia africana Lindl.		42	GJ91
A. gigantea Rchb. f.		42	GJ91
A. nilotica N.E. Br.		42	TK84
Cymbidiella flabellata Rolfe		52	GJ91
C. pardalina (Rchb. f.) Garay		52	GJ91
C. rhodochila Rolfe		54	TK84
Cymbidium aliciae Quis.		40	GJ91
C. aloifolium (L.) Sw.		40	G84, G85, GJ91
	20		G88
C. atropurpureum (Lindl.) Rolfe		40	F69
C. bicolor Lindl.	20		TK84
C. canaliculatum R. Br.		40	GJ91
C. chloranthum Lindl.		40	GJ91
C. cochleare Lindl.		40	TK84, G85
C. cyperifolium Wall.		40	G84, G85
C. dayanum Rchb. f.		40	GJ91, GJ96
C. dayanum var. *austro-japonicum*		40	TK84
C. devonianum Paxt.		40	TK84, G85, GJ91
	20		TK84
C. eburneum Lindl.		40	TK84, G85, GJ91
C. elegans Lindl.		40	G85, GJ91
C. ensifolium (L.) Sw.		40	TK84, GJ91, GJ96
C. erythrostylum Rolfe		40	F69, GJ91
C. faberi Rolfe		40	GJ91
C. finlaysonianum Wall. ex Lindl.		40	F69, GJ91
C. floribundum Lindl.		40	GJ90, GJ91, GJ96
C. formosanum Hayata (= *C. goeringii*)		40	G85
C. forrestii Rolfe (= *C. goeringii*)		40	F69
C. gammieanum King & Pantl.		40	G85
C. giganteum Wall. ex Lindl.		40	TK84, G85, GJ94
	20		G84
	40		G88
C. goeringii (Rchb. f.) Rchb. f.		40	GJ91, GJ96
C. grandiflorum Griff. (= *C. hookerianum*)		40	F69, G84

Continued

Table II - Continued

Taxon	n	2n	Sources
Cymbidium hookerianum Rchb. f.		40	GJ91, GJ96
C. hookerianum var. *lowianum* (Rchb. f.) Y.S.Wu			
& S.C. Chen		38	GJ91, GJ96
C. insigne Rolfe		40	F69, GJ91
C. iridifolium A. Cunn. (= *C. madinum*)		40	F69
C. iridioides D. Don		40	GJ91
C. javanicum Blume	19	38	GJ91
C. kanran Makino		40	TK84, G85, GJ91
C. lancifolium Hook. f.		40	G85, GJ91
	20		TK84
		38	TK84, GJ91
C. longifolim D. Don		40	G85, GJ91
C. lowianum Rchb. f.	20		M73, TK84
		40	M77, TK84, GJ91
C. lowianum var. *concolor*		40	TK84
C. macrorhizon Lindl.	19		TK84
	19	38	GJ91
C. madinum Lindl.		40	GJ91
C. mastersii Griffith		40	F69, G85, GJ91
C. munronianum King & Pantl. (= *C. ensifolium*)		40	F69
C. nagifolium Masamune (= *C. lancifolium*)		40	F69
		38	F69
C. nipponicum (Franch. & Sav.) Rolfe (= *C.*			
macrorhizon)		38	GJ91
C. parishii Rchb. f.		40	F69, GJ91
C. parishii var. *sanderae*		40	TK84
C. pauwelsii		80	F69
C. pendulum Sw. (= *C. aloifolium*)		40	M73, G85, GJ91, GJ96
	20		TK84, G84
C. pumilum Rolfe (= *C. floribundum*)		40	TK84
C. rubrigemmum Hayata (= *C. ensifolium*)		40	G85
C. schroederi		40	TK84
C. simonsianum King & Pantl. (= *C. dayanum*)		40	TK84
C. sinense (Andr.) Willd.		40	TK84, G85, GJ91, GJ96
C. tigrinum Parish ex O'Brien		40	G85, GJ91
C. tracyanum Hort. ex Lindl.		40	TK84, GJ91
C. virescens Lindl. (= *C. goeringii*)		40	TK84
C. whiteae King & Pantl.		40	G85, GJ91
Cymbidium sp.		40	GJ96
Cymbidium sp.		40	GJ96
Cymbidium spp.		40	G84
Cyrtopodium andersonii (Andrews) R. Br.		46	GJ91
C. blanchetii Rchb. f.		92	PW
C. eugenii Rchb. f.	22		PW
C. gigas (Vell.) Hoehne		46	PW
C. inaldianum L.C.Menezes		46	PW

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Table II - Continued

Taxon	n	2n	Sources
Cyrtopodium intermedium Brade	23	46	PW
C. paranaense Schltr.		46	PW
C. punctatum (L.) Lindl.		46	GJ91
Eulophiella roempleriana Schltr.		52	GJ91
E. rolfei Hort.		52	GJ90, GJ91
Galeandra baueri Lindl.		56	GJ91
G. devoniana Schomb. ex Lindl.		56	GJ91
Grammangis devoniana Schomb. ex Lindl.		56	GJ91
G. allisii Rchb. f.		54	TK84, GJ91
Grammatophyllum scriptum (Lindl.) Blume		40	TK84, GJ91
G. speciosum Blume		40	TK84, GJ91
G. stapeliiflorum (Teijsm. & Binn.) J.J. Smith		40	GJ91
Graphorckis lurida (Sw.) Kuntze		52	G84
G. scripta (Thouars) Kuntze		54	GJ91
Grobya amhersitiae Lindl.		54	GJ91
G. galeata	28		B57
Subtribe Acriopsidinae			
Acriopsis javanica Reinw		40	GJ91
Subtribe Catasetinae Schltr.			
Catasetum atratum Lindl.		ca. 108	TK84
C. barbatum Lindl.		54	PW
C. callosum Lindl.		54	M73
C. cassideum Linden & Rchb. f.		54	M73
C. cernum (Lindl.) Rchb. f.		54	M73
C. deltoideum Lindl.		ca. 54	M73
C. discolor Lindl.		108	M73
C. fimbriatum (C. Morren) Lindl.		108	M73
C. fimbriatum var. inconstans Mansf.		108	M73
C. fimbriatum var. morrenianum Mansf.		ca. 108	M73
C. integerrimum Hook.		54	M73
C. luridum (Link) Lindl.		ca. 54	M73
		54	PW
C. macrocarpum Rich.		54	M73, PW
C. pileatum Rchb. f.		ca. 108	M73
C. pileatum Rchb. f.		ca. 162	TK84
C. planiceps Lindl.		ca. 162	TK84
		ca. 108	TK84
C. purum Nees ex Simmings		54	M73, PW
C. russelianum		54	TK84
C. thylaciochilum Lam.		54	M73
C. trulla Lindl.		54	M73
C. viridiflavum Hook.		54	M73
C. warscewiczii Lindl.		54	M73
Cychnoches chlorochilon Kltz.		68	M73
C. egertonianum Batem.		ca. 68	M73
C. loddigesii Lindl.		64	M73

Continued

Table II - Continued

Taxon	n	2n	Sources
Cychnoches ventricosum Batem.		68	M73
Mormodes buccinator Lindl.		54	M73
M. buccinator var. citrinum		54	M73
M. histrio Lindl. & Rchb. f.		54	M73
M. rolfeanum Linden		54	GJ94
TRIBE MAXILLARIEAE			
Subtribe Zygopetalinae Schltr.			
Dichaea muricata (Sw.) Lindl. var. *neglecta*		52	TK84
D. panamensis Lindl.		52	PW
Koelensteinia graminea (Lindl.) Schltr.	ca. 48		TK84
K. tricolor (Lindl.) Rchb. f.		ca. 96	PW
Promenaea citrina Don.		46	TK84
Warrea costaricensis Schltr.		52	GJ91
Zygopetalum citrinum Lodd.		96	TK84
Z. discolor (= *Warczewiczella discolor*)		ca. 48	TK84
Z. mackayi Hook.	ca. 24		TK84
Z. maxillare Lodd.		48	TK84
Z. odoratissimum		48-50	TK84
Subtribe Lycastinae Schltr.			
Bifrenaria harrisoniae (Hook.) Rchb. f.		40	TK84
		38	TK84
B. magnicalcarata (Hoehne) Pabst		80	PW
Lycaste aromatica Lindl.	20		TK84
L. aff. *macrophylla* (Poepp. & Endl.) Lindl.		ca. 48	GJ94
Xylobium foveatum (Lindl.) Nichols		40	PW
X. variegatum (Ruíz & Pavon) Garay & Dunst.		40	G85
Subtribe Maxillariinae			
Maxillaria discolor (Lodd. ex Lindl.) Rchb. f.		42	PW
M. laevilabris Lindl.		42	GJ94
M. picta Hook.		40	TK84
M. rufescens Lindl.		40	PW
M. tenuifolia Lindl.		40	TK84
M. violaceo-punctata Rchb. f.		42	G85
Trigonidium acuminatum Batem. ex Lindl.		40	PW
T. obtusum Lindl.		40	PW
Subtribe Stanhopeinae Benth.			
Acineta superba (H.B.K.) Rchb. f.		40, 42	M73
Coryanthes maculata Hook.		40	M73, GJ96
C. speciosa Hook.		40	PW
Gongora galeata Rchb. f.	20		TK84
G. quinquenervis Ruíz & Pavon		40	TK84, G85, PW
G. tricolor Rchb. f.		40	TK84
G. truncata Lindl.		ca. 38	M73
Peristeria alata var. *gattonensis*		40	M73
P. guttata Kn. & Westc.		40	M73
Stanhopea bucephalus Lindl.		40	M73

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Table II - Continued

Taxon	n	2n	Sources
Stanhopea candida Rodr.		40	M73
S. costaricensis Rchb. f.		40	M73
S. devoniensis Lindl.		40	M73
S. ecornuta Lem.		ca. 40	M73
S. gibosa Rchb. f.		40	M73
S. grandiflora Lindl.		40	M73
S. graveolans Lindl.		40	M73
S. inodora Rchb. f.		40	M73
S. insigins Frost ex Hook.	20		TK84
S. oculata (Lodd.) Lindl.	20	40	M77
S. peruviana Rolfe		42	M73
S. ruckeri Lindl.		40	M73
S. saccata Batem.		ca. 40	M73
S. tigrina Batem. (= *S. hernandezii*)	20		TK84
		40	M73
		80	M77
		40	M73
S. *wardii* Lodd. & Lindl.		41, 42	M73
Subtribe Ornithocephalinae			
Dipteranthus duchii Pabst		56	PW
Dipteranthus sp.		56	PW
Subtribe Oncidiinae			
Ada chlorops (Endres & Rchb. f.) Williams	30		GJ91
A. elegantula		60	TK84
Ada sp.		60	TK84
Aspasia epidendroides Lindl.		60	TK84
A. principissa Rchb. f.		60	TK84
A. pusila Schweinf.		56	TK84
Brassia allenii Williams ex Schweinf.		50	M77
B. caudata Lindl.		60	M73, M77
B. chloroleuca Rodr.		60	M73
B. gireoudiana Rchb. f. & Warm.		60	M73, M77
B. lawrenciana Lindl.		60	PW
B. longissima Schltr.		60	M73
B. maculata R. Br.		60	M73, M77
B. pumila Lindl.		60	M77
B. verrucosa Lindl.		60	M73
B. verrucosa var. *grandiflora*		56	TK84
Comparettia falcata Poepp. & Endl.		42	TK84
		44	TK84
C. speciosa Rchb. f.		42	TK84
Ionopsis utricularioides (Sw.) Lindl. (as *I. paniculata* Lindl.)	23		B57
Gomesa crispa (Lindl.) Kl. & Rchb. f.		56	TK84
G. recurva R. Br.		56	M73
Lockartia oerstedii Rchb. f.		14	TK84

Continued

Table II - Continued

Taxon	n	2n	Sources
Lockartia goyazensis Rchb. f.		56	PW
L. micrantha Rchb. f.		56	CK75
Macradenia brassavolae Rchb. f.		48	TK84
M. paraensis Barb. Rodr.	26		B57
Miltonia bluntii Rchb. f.		60	M73
M. festiva Nichols		59	M73
M. flavescens Lindl.		60	M73, PW
M. regnellii Rchb. f.		60	M73
M. roezlii Nichols. var. *alba*		56	M73
		60	M73
M. spectabilis Lindl.		60	M73
M. spectabilis var. *lineata*		56	M73
M. spectabilis var. *moreliana* subvar. *rosea*		56	M73
M. vexillaria Batem.		60	M73
M. warscewiczii Rchb. f.		56	M73
M. warscewiczii var. *panamensie*		56	M73
Notylia bicolor Lindl.		42	TK84
N. lyrata S.P. Moore		44	PW
N. panamensis Ames		42	TK84
Odontoglossum auriculatum Rolfe		56	GJ91
O. cosntrictum Lindl.		56	GJ91
O. cariniferum Rchb.		56	M77
O. citrosmum		44	TK84
O. cordatum Lindl.		56	M73
O. crispum Lindl.		56	TK84
		112	GJ91
O. cruentum Rchb. f.		56	GJ91
O. grande Lindl.		44	M77
O. hallii Lindl.		56	GJ91
O. harryanum Rchb. f.		56	GJ91
O. insleayi Lindl.		44	TK84
O. ioplocon Rchb. f.		56	GJ91
O. kegelijani E. Morr.		56	TK84
O. lindenii Lindl.		112	GJ91
O. lindleyanum var. *validum*		56	GJ91
O. luteo-purpureum Lindl.		56	GJ91
O. mirandanum Rchb. f.		56	GJ91
O. naevium Lindl.		56	GJ91
O. nobile Rchb. f.		56	GJ91
O. odoratum Lindl.		56	GJ91
O. pardinum Lindl.		56	GJ91
O. pendulum Batem.		44	TK84
O. reversum Bockem.		56	GJ91
O. sceptrum Rchb. f. & Warsc.		56	GJ91
O. schllieperianum Rchb. f.		44	TK84
O. stenoglossum (Schltr.) Williams ex Correll		56	M77

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Table II - Continued

Taxon	n	2n	Sources
Odontoglossum tripudians Rchb. f. & Warsc.		56	GJ91
O. wallisii Linden & Rchb. f.		56	GJ91
Oncidium altissimum Sw.		56	M73
O. ampliatum Lindl.		44	M73, M77
O. annhadderiae		42	TK84
O. ansiferum Rchb. f.		56	M73, M77
O. anthocrene Rchb. f.		56	M73
O. aurosum Rchb. f. & Warm.		54	TK84
O. bahamense Nash		84	M77
O. barbatum Lindl.	28		B57
		56	PW
O. baueri Lindl.		56	M73, M77, PW
O. bicallosum Lindl.	14		TK84
		28	M77
O. blanchetii Rchb. f.		ca. 112	PW
O. brachyandrum Lindl.		56	M73
O. brunleesianum Rchb. f.		56	TK84
O. calochilum Cogn.		42	TK84
O. carthaginense (Jacq.) Sw.		30	M73, M77
O. carthaginense var. *roseum*		30	TK84
O. cavendishianum Batem.	14		B57
O. cebolleta Sw.	18		B57
		36	TK84, PW
		36, 72	TK84
O. cheirophorum Rchb. f.		56	TK84
O. cordeanum		56	TK84
O. crispum Lodd.		56	TK84, PW
O. cubense		56	TK84
O. cucculatum Lindl.		54	TK84
O. curtum Lindl.		52	TK84
O. desertorum		40	M77
O. ebrachiatum Ames & Schweinf.		28	TK84
O. ensatum Lindl.		56	M77
O. excavatum Lindl.		56	M73
O. flexuosum Sims		56	TK84, PW
O. aff. *flexuosum* Sims		ca. 168	PW
O. floridanum Ames		56	M77
O. floridephillipsiae Moir & Hawkes		126	TK84
O. gravesianum Rolfe		56	PW
O. globuliferum H.B.K.		56	M73
O. guttatum Rchb. f.		28	M73
O. haematochilum Lindl.		28	M77
O. harrisonianum Lindl.		42	M73
O. hastatum Lindl.		56	M73
O. henekenii Sch.		40	M73, M77
O. hieroglyphicum Rchb. f.		56	TK84

Continued

Table II - Continued

Taxon	n	2n	Sources
Oncidium hyphaemacticum Rchb. f.		56	M73
O. incurvum Barker		56	M73
O. inouei Hashimoto		56	GJ94
O. intermedium Knowl. & Westc.		40	M73
O. intermedium "gigas"		40	M73
O. isthmi Schltr.		56	M73
O. jimenezii		42	M73
O. jonesianum Rchb. f.		30	TK84
O. kenscoffii Moir		84	M73
O. kramerianum Rchb. f.		38	TK84
O. lammeligerum Rchb. f.		55-57	TK84
O. lanceanum Lindl.		28	M73, M77
O. lemonianum Lindl.		42	TK84
O. leuchochilum Batem		56	TK84
O. lieboldii Rchb. f.		40	TK84
O. loefgrenii Cogn.	28	56	PW
O. longifolium Lindl.		28	TK84
O. longipes Lindl. & Paxt.	28		B57
O. loxense Lindl.		56?	TK84
O. lucayanum Nash		40	TK84
O. luridum Lindl.		28	TK84
		30	M77
O. maculatum Beer		56	M73
O. marshallianum Rchb. f.		56	TK84
O. microchilum Batem.		36	TK84
O. micropogon Rchb. f.		56	TK84
O. nanum Lindl.		26	M73, TK84
O. nebulosum Lindl.		56	TK84
O. nigratum Lindl.		56	TK84
O. nudum Batem.		36	M77, TK84
O. obryzatoides Krzl.		56	M73, TK84
O. obryzatum Rchb. & Warsc.		56	M73, TK84
O. oestlundianum		28	TK84
O. onustum Lindl.		56	M73, M77
O. ornithorrhynchum H.B.K.		56	M73, TK84
	28		TK84
O. panamense Schltr.		56	M73, TK84
O. papilio Lindl.		38	M73, M77
O. paranaense Krzl.		56	PW
O. parviflorum		56	TK84
O. pentadactylon Lindl.		40-42	TK84
O. phalaenopsis Lind. & Rchb. f.		56	TK84
O. phymatochilum Lindl.		56	M73
O. polyandenium Lindl.		56	M73
O. pawellii Schltr.		56	M73
O. praetextum Rchb. f.	28		TK84

Continued on the next page

Table II - Continued

Taxon	n	2n	Sources
Oncidium pulchelum Hook.		42	M73, M77
O. pulvinatum Lindl.		42	M77
O. pumillum Lindl.		30	TK84, PW
O. quadrilobum		40	TK84
O. robustissimum Rchb. f.		44	TK84
O. sarcodes Lindl.		56	M77
O. scandens Moir		84	TK84
O. sylvestre Lindl.		84	M73
		126	TK84
O. sphacelatum Lindl.		38	GJ90, GJ91
O. splendidum A. Reich.		36	M73, M77
O. stenotis Rchb. f.		56	M73, M77
O. stipitatum Lindl.		36	M77, GJ91
O. stramineum Batem.		30	TK84
O. teres Ames & Schweinf.		28	TK84
O. tetrapetalum		42	TK84
O. tetraskelidon Krzl.	28		TK84
O. tigrinum La Llave & Lex		56	M77
O. trilobum (Schltr.) Garay & Stacy		56	GJ94
O. triquetrum R. Br.		42	M73, M77
O. urophyllum Lodd.		84	M73
O. varicosum Lindl.	28		TK84
		56	TK84
		112, 168	TK84
O. varicosum Lindl.	56		B57
	56	112	PW
O. varicosum var. *rogersii*		56	TK84
O. variegatum Sw.		42	M77
O. varvelum		63	TK84
O. velutinum Lindl. & Paxt.		84	TK84
O. volvox Rchb. f.	28		TK84

Continued

Table II - Continued

Taxon	n	2n	Sources
Oncidium warmingii Rchb. f.		140	TK84
O. wentworthianum Batem.		56	M73, TK84
Oncidium sp.		40	M73, TK84
Oncidium sp.		40	M73, TK84
Oncidium sp.		133	M73, TK84
Oncidium sp.		60	GJ94
Psygmorchis glossomystax (Rchb. f.) Dodson & Dressler (as *Oncidium glossomistax* Rchb. f.)		14	TK84
P. pusilla (L.) Dodson & Dressler (as *O. psillum* L.)		10, 14	TK84
	6	12	PW
Rodriguezia bahiaensis Rchb. f.		42	PW
R. batemani Lindl		42	TK84
R. decora (Lem.) Rchb. f		42	TK84
R. lanceolata Ruíz & Pavon		42	TK84, PW
R. fragrans (Lindl.) Rchb. f.		42	TK84
R. strobelii Garay		42	TK84
R. teuscherii Garay		28, 29	TK84
R. venusta Rchb. f.		42	TK84
Sigmatostalix radicans (Rchb. f.) Garay & Pabst		56	TK84
		60	TK84
Trichocentrum albo-purpureum Lindl. & Rchb. f.		24, 28	TK84
T. capistratum Lindl. & Rchb. f.		28	TK84
T. cornucopiae Lindl. & Rchb. f.		20	PW
T. maculatum Lindl.		24	TK84
T. panamense Rolfe		28	TK84
T. tigrinum Lindl. & Rchb. f.		24	TK84
Thrichopilia marginata Henfr.		56	TK84

B57 = Blumenschein, 1957; F69 = Fedorov, 1969; M73 = Moore, 1973; M74 = Moore, 1974; M77 = Moore, 1977; TK84 = Tanaka and Kamemoto, 1984; G84 = Goldblatt, 1984; G85 = Goldblatt, 1985; G88 = Goldblatt, 1988; GJ90 = Goldblatt and Johnson, 1990; GJ91 = Goldblatt and Johnson, 1991; GJ94 = Goldblatt and Johnson, 1994; GJ96 = Goldblatt and Johnson, 1996; PW = Present work.

Some chromosome numbers registered in the literature were not included in Tables II and III because they clearly differed from other records for the same species or were incompatible with the records for the genus. For example, Blumenschein (1957, 1960a) reported n = 28 in the pollen mitosis of four *Catasetum* species. However, in Jones and Daker's (1968) analysis of 21 taxa of this genus, including three of the four species reported by Blumenschein, none presented this number. Further in the present work, 2n = 54, the most common number in the genus, was observed in four species (Figures 1h,i and 2a-c) and 2n = ca. 108 in two populations of *Catasetum discolor*. All the counts considered as probably wrong were presented in a separate table (Table IV) and were not included in the discussion.

Numerical variations related to a single species were excluded from Table II, wherever other references confirmed only one of these numbers. In *Oncidium microchilum*, for example, Sinotô (1962, 1969) and Charanasri

Table III - Chromosome numbers and probable base numbers of tribes, subtribes and genera of Cymbidioid (*sensu* Dressler, 1993). Chromosome numbers are ordered from the more to the less frequent. Numbers conected with a line have equal frequencies.

Tribes and subtribes with the number of genera/species known	Genera with the number of species known/ analyzed	Chromosome numbers reported and more probable base numbers (underlined)
Tribe Malaxideae (6/960)		
	Liparis Rich. (350/52)	21, 15, 19, 10-20, 14-18-40, 11-13-ca.21-28-34-38
	Malaxis Sw. (300/13)	21, 15-30, 14, 18-ca. 20-22
	Oberonia Lindl. (300/30)	15, 30
Tribe Calypsoeae (9/35)		
	Calypso Salisb. (1/1)	14
	Corallorhiza Chatelain (15/5)	21, 20-42
	Cremastra Lindl. (7/4)	24, 26
	Dactylostalix Rchb. f. (1/1)	21
	Ephippianthus Rchb. f. (1/1)	18-20-21
	Oreorchis Lindl. (9/2)	24-42
Tribe Cymbidieae (28/732)		
Subtribe Eulophiinae (6/264)		
	Dipodium R. Br. (20/1)	23
	Eulophia R. Br. (200/39)	27, 28, 16-21, 24, 20-25, 22-30, 14-26-31-33-34-35-36-37-38-40-41-44-47-48-50-56-60
	Oeceoclades Lindl. (31/2)	29, 24-27
Subtribe Cyrtopodiinae (12/139)		
	Anselia Lindl. (2/3)	21
	Cymbidiella Rolfe (3/3)	26, 27
	Cymbidium Sw. (45/40)	20, 19, 40, 43/2, 57/2
	Cyrtopodium R. Br. (30/8)	23, 22-46
	Eulophiella Rolfe (2/2)	26
	Galeandra Lindl. (25/1)	28
	Grammangis Rchb. f. (2/2)	27-28
	Grammatophyllum Blume (12/3)	20
	Graphorkis Thouars (5/2)	26-27
	Grobya Lindl. (3/2)	27-28
Subtribe Acriopsidinae (1/6)		
	Acriopsis Blume (6/1)	20
Subtribe Catasetinae (5/194)		
	Catasetum Rich. ex Kunth (100/19)	27, 54, ca. 54, ca. 27-81
	Cychnoches Lindl. (23/4)	34, 32-ca. 34
	Mormodes Lindl. (60/3)	27
Tribe Maxillarieae (157/2.573)		
Subtribe Zygopetalinae (30/331)		
	Dichaea Lindl. (55/2)	26
	Koelensteinia Rchb. f. (16/2)	ca. 48
	Promenaea Lindl. (14/1)	23
	Warrea Lindl. (4/1)	26
	Zygopetalum Hook. (15/5)	ca. 24, 48, 25
Subtribe Lycastinae (8/127)		
	Bifrenaria Lindl. (24/2)	19-20-40
	Lycaste Lindl. (49/2)	20-ca. 24
	Xylobium Lindl. (29/2)	20
Subtribe Maxillariinae (8/472)		
	Maxillaria Ruiz & Pavon (420/6)	20-21
	Trigonidium Lindl. (14/2)	20

Continued on the next page

Table III - Continued

Tribes and subtribes with the number of genera/species known	Genera with the number of species known/ analyzed	Chromosome numbers reported and more probable base numbers (underlined)
Subtribe Stanhopeinae (22/248)		
	Acineta Lindl. (20/1)	20-21
	Coryanthes Hook. (20/2)	20
	Gongora Ruíz & Pavon (50/4)	20, ca. 19
	Peristeria Hook. (15/2)	20
	Stanhopea Frost ex Hook. (55/17)	20, ca. 20-21, 40
Subtribe Ornithocephaliinae (14/76)		
	Dipteranthus Barb. Rodr. (8/2)	28
Subtribe Oncidiinae (47/1231)		
	Ada Lindl. (15/3)	30
	Aspasia Lindl. (8/3)	30, 28
	Brassia R. Br. (35/9)	30, 26, 25
	Comparettia Poepp. & Endl. (10/2)	21, 22
	Gomesa R. Br. (13/2)	28
	Ionopsis Kunth (3/1)	23
	Leochilus Knowles & West. (10/3)	21, 24
	Lockartia Hook. (24/3)	28, 7
	Macradenia R. Br. (12/2)	24-26
	Miltonia Lindl. (25/8)	30, 28, 59/2
	Notylia Lindl. (50/3)	21, 22
	Odontoglossum Kunth (140/28)	28, 22, 56
	Oncidium Sw. (420/113)	28, 21, 14, 42, 15-18, 19-22-26-27-56-84, 13-30-63-70-57/2-63/2
	Sigmatostalix Reichb. (35/1)	28-30
	Psygmorchis Dodson & Dressler (5/2)	7, 5, 6
	Rodriguezia Ruíz & Pavon (40/8)	21, 14
	Trichocentrum Poepp & Endl. (30/6)	12-14, 10
	Trichopilia Lindl. (30/1)	28

et al. (1973) registered 2n = 36, 37. As the number 2n = 37 was not found in any species of *Oncidium* and 2n = 36 was confirmed by other authors for this species, 2n = 37 was excluded from Table II. The number 2n = 41 for *Eulophia euglossa* was also removed because it was described as an occasional trisomy besides the normal number 2n = 40 (ar-Rushdi, 1971). Similarly, numbers attributed to B chromosomes, like the reference of Aoyama and Tanaka (1988) for a single individual with 2n = 39 + 5Bs of *Cymbidium javanicum* and 2n = 38 + 1 in *C. lancifolium*, were excluded. Occasional triploids, like that referred to *C. javanicum* (2n = 57) by the same authors above, were not considered significant for the cytotaxonomic evaluation of the genus and were also excluded. All these counts were listed in Table IV for future evaluation. Some other seemingly incorrect counts were not excluded for a lack of documentation or a strong argument proving the error. Daker and Jones (1969), for example, suggested that counts with 2n = 42 in the subtribe Stanhopeinae are "largely the result of detached satellites", but they admit that at least *Stanhopea peruviana* has 2n = 42. In this case all the counts of 2n = 42 were excluded in only *S. grandiflora*, *S. inodora*, *S. oculata* and *S. tigrina*, because other counts are known that confirm 2n = 40 for these species. In *S. wardii* and *Acineta superba*, the only records known were conserved (2n = 41, 42 and 2n = 40, 42, respectively). This "cleaning", albeit partial, reduced the importance of those numbers in the identification of the base number of *Stanhopea* and Stanhopeinae.

Karyological evolution

The chromosome number variability observed in orchids is not only very extensive but also difficult to relate to a single base number. Cytotaxonomical analysis can be better understood in genera with great cytological diversity, which often correspond to the genera with the highest number of species in the tribe or family, like *Boronia* in the tribe Boroniae, Rutaceae (Stace, 1995), *Carex* in Cyperaceae (Luceño, 1994), and *Passiflora* in Passifloraceae (Snow and MacDougal, 1993). In Cymbidioid, the largest genera are *Oncidium* and *Maxillaria* with about 420 species in each one. *Maxillaria* is very poorly investigated (only six species), whereas *Oncidium* is the genus most extensively studied of the phylad (117 species). Chromosome number variability in *Oncidium* is also quite representative of the group. The known haploid numbers are n = 13, 14, 15, 18, 19, 20, 21, 22, 25, 26, 27, 28, 29, 30, 36, 42, 56, 63, 70, 84. This variation is clearly dominated by the polyploid series n = 14, 21, 28, 42, 56, 63, 70, 84. The great majority (64.8%) are ortoploid with n = 14, 21 or 28, of which 46% display n = 28. These data strongly suggest x_1 = 7 as the primary base number for the genus, al-

Table IV - Cymbidioid species with uncertain chromosome numbers.

Species	n	2n	Index	Species	n	2n	Index
Aspasia principissa Rchb. f.		58	TK84	*Liparis rostrata* L.	15		TK84
Brassia lawrenciana var. *longissima*		52-56	TK84	*Malaxis monophylla* (L.) Sw.	15-17		TK84
B. verrucosa Lindl.		52-58	TK84	*Miltonia flavescens* Lindl.		56	TK84
Calypso bulbosa (L.) Oakes		32	TK84	*Oberonia caulescens* Lindl.	13		TK84
Catasetum atratum Lindl.		56	TK84	*O. myriantha* Lindl.	ca. 36		TK84
C. cernum (Lindl.) Rchb. f.		56	TK84	*Odontoglossum citrosmum*		44-48	TK84
C. hookeri Lindl.		56	TK84	*O. grande*		60?	TK84
C. macrocarpum L.C. Rich.		56	TK84	*O. harryanum* Rchb. f.		84	GJ91
Corallorhiza trifida Chatel		38	G84	*Oeceoclades maculata* (Lindl.) Lindl.		48	GJ90
		40	G88	*Oncidium baueri* Lindl.		ca. 52	TK84
Cremastra appendiculata (D. Don) Makino		42	G88	*O. cartagenense* (Jacq.) Sw.		28	TK84
C. unguiculata		50	TK84	*O. cebolleta* Sw.		34	TK84
C. variabilis Nakai		46	TK84	*O. cheirophorum* Rchb. f.		ca. 48	TK84
Cymbidium aloifolium Sw.	16	32	TK84	*O. guttatum* Rchb. f. var. *olivaceum*		32	TK84
C. bicolor Lindl.		42	GJ90	*O. haematochilum* Lindl.		40	TK84
C. cyperifolium Lindl.		42	TK84	*O. inouei* Hashimoto		52	GJ94
		36, 40	GJ96	*O. lanceanum* Lindl.	13	26 (24)	TK84
C. eburneum Lindl.		38	GJ91, GJ96	*O. lammerigerum*		55-47	TK84
C. faberi Rolfe		43, 44	GJ96	*O. lieboldii*		42	TK84
		42	GJ91	*O. luridum* Lindl.		32	TK84
C. floribundum Lindl.		38	GJ91			28 + 2f	TK84
C. goeringii (Rchb. f.) Rchb. f.		38	GJ91	*O. macrantum* Lindl.		50-57	TK84
C. hookerianum Rchb. f.		38	GJ91	*O. microchilum* Batem.		37	TK84
C. javanicum Blume		43, 57	GJ91	*O. sphacelatum* Lindl.		57	GJ91
C. kanran Makino		40, 41	GJ91			56	M73
C. lancifolium Hook. f.		39	GJ91	*O. splendidum* A. Reich.		34	TK84
C. lowianum Reichb. f.	9-10		TK84	*O. stipitatum* Lindl.		28	TK84
C. sikkimense Hook. f.	19		TK84	*O. stramineum* Batem.		28	TK84
Cymbidium sp.		42	GJ96	*O. tigrinum*		54	TK84
Eulophia clavicornis Lindl.	47		TK84	*O. variegatum* Sw.		40	TK84
E. euglossa (Rchb. f.) Rchb. f.		41	TK84	*O. warmingii* Rchb. f.		150	TK84
E. ovalis Lindl. subsp. *bainensis* (Rolfe) Hall		41	TK84	*Oreorchis patens* (Lindl.) Lindl.	50		TK84
Gongora quinquenervis Ruíz & Pavon		38, 40	TK84	*Rodriguezia teuscherii* Garay		29	TK84
Grammatophyllum scriptum (Lindl.) Blume		38	G88	*Stanhopea grandiflora* Lindl.		38, 42	TK84
Liparis krameri Franc. & Savat.		36	GJ94	*S. inodora* Rchb. f.		42	TK84
Liparis nervosa (Sw.) Lindl.		40	GJ91, GJ96	*S. oculata* (Lodd.) Lindl.		42	TK84
L. paradoxa Rchb. f.	18		TK84	*S. tigrina* Batem. (= *S. hernandezii*)		41, 42	TK84
L. paradoxa Rchb. f.	18		TK84				

though this number is hypothetical, since no species of the genus is known with n = 7. Thus, most *Oncidium* species should be tetraploid (n = 14), hexaploid (n = 21) or octoploid (n = 28). The diploids have not yet been found or were extinct, since the hexaploid n = 21 could only arise from a cross between tetraploids (n = 14) and putative diploids (n = 7) followed by polyploidization (Harlan and De Wet, 1975). Therefore, if the genus was originated from a tetraploid lineage, the hexaploid species could not belong to this same lineage and the genus would be artificial. The same may have occurred in *Rodriguezia*, with 2n = 28 (Sinotô, 1962) and 2n = 42 (Figure 4a,b, Table II).

When the subtribe Oncidiinae is considered as a whole, the variation of chromosome numbers seems very similar to that of the genus *Oncidium* (Figure 6), with the numbers n = 21 and n = 28 prevailing, suggesting that the other genera have a common ancestor with *Oncidium*. The subtribe also has the smallest chromosome numbers of the family: n = 7 in *Lockartia* and n = 5, 6 and 7 in *Psygmorchis*. In three populations of *P. pusilla* studied in the present work, 2n = 12 and n = 6 were always found (Figure 3g), disagreeing with records of Dodson (1957a,b) and Kugust (1966, *apud* Tanaka and Kamemoto, 1984). Further analyses in other *Lockartia* species would be important to verify whether the polyploid series observed in *Oncidium* is also repeated in this genus. The only *Lockartia* species analyzed in the present work exhibited 2n = 56 (Figure 4d), which coincides with the previous reports of Charanasri and Kamemoto (1975) for *L. micrantha*. These data support the inclusion of *Lockartia* in Oncidiinae, in opposition to the assumption of Freudenstein and Rasmussen (1999) based on the absence of leaf articulation in this genus.

Considering the polyploid series observed in *Oncidium* and Oncidiinae in general, it is reasonable to suppose that x = 7 would be the primary base number of the subtribe, as suggested by Charanasri and Kamemoto (1975). In this case, most Oncidiinae genera would have hexaploid (*Comparettia*, *Notylia*) or octoploid origin (*Aspasia*, *Gomesa*, *Miltonia*, *Sigmatostalix*, *Trichopilia*). The number n = 7 may represent the original haploid complement of

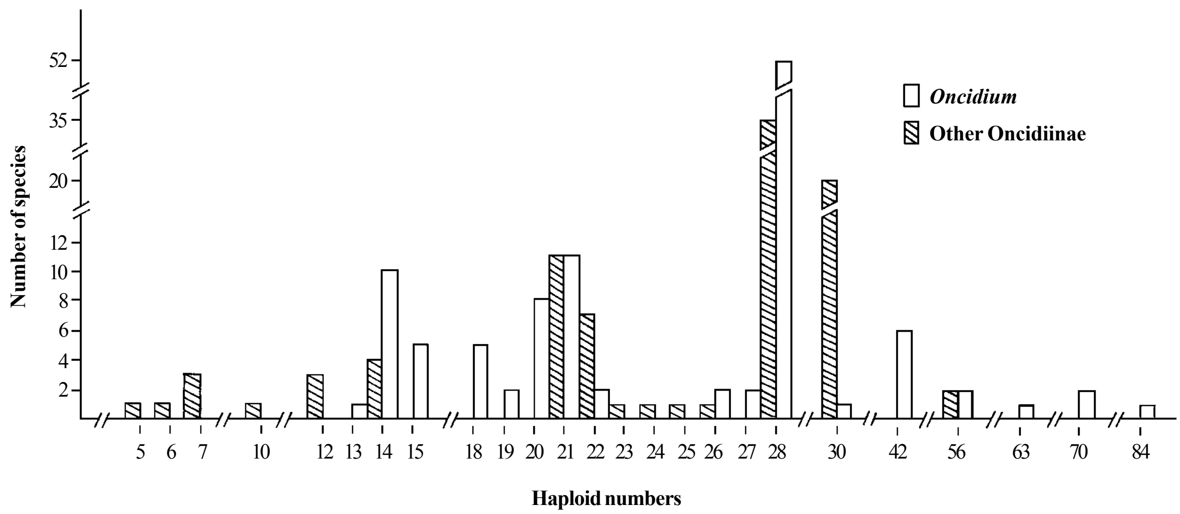

Figure 6 - Chromosome number variation among *Oncidium* species compared to other Oncidiinae.

Orchidaceae, found nowadays in very few species. Successive cycles of polyploidy would have originated tetraploid (n = 14), hexaploid (n = 21) and octoploid (n = 28) lineages, some of which gave origin to entirely polyploid genera (Table III). As polyploidy is quite a recurrent phenomenon in the evolution of angiosperms (Soltis and Soltis, 1995; Leitch and Bennett, 1997), it is very probable that higher polyploids arose *de novo* many times in a number of other genera.

The only cytologically known genera distant from the series n = 7, 14, 21, 28 in Oncidiinae are *Ionopsis*, *Macradenia* and *Trichocentrum*. In *Ionopsis*, there is only one record with n = 23, whereas in *Macradenia* there are data for one species with n = 26 and another with 2n = 48 chromosomes (Blumenschein, 1957; Sinotô, 1962). In *Trichocentrum*, there are records of five species with 2n = 28 and 2n = 24, besides the present count with 2n = 20 in *T. cornucopiae* (Figure 3h). *Trichocentrum* may have a dysploid series with n = 14, 12, 10, but the available data are still very fragmented. Chase (1986), based on a combination of floral, vegetative and chromosomal characters, suggested that *Trichocentrum* could represent an independent evolutionary lineage distinct from the other genera of Oncidiinae.

The present interpretation for the karyological evolution of *Oncidium*/Oncidiinae conflicts directly with that of Chase and collaborators (Chase, 1986, Chase and Pippen, 1988; Chase and Olmstead, 1988; Chase and Palmer, 1992). These authors observed that the most primitive representatives of the subtribe had higher chromosome numbers, whereas *Psygmorchis* and *Lockartia*, with more derived morphological characters, like laterally flattened leaves, displayed the lowest chromosome numbers. Therefore they concluded that *Oncidium* and some Oncidiinae have the original chromosome numbers (x = 28, 30) which, through successive dysploidy, originated the low numbered species with n = 7-5. This conclusion was supported by isoenzymatic evidence from representatives of this group, which almost always exhibited a single locus for each isozyme (Chase and Olmstead, 1988), like dysploids. However, the isoenzymatic analysis of several other definitely polyploid taxa also displayed a similar pattern (Haufler, 1987), suggesting that it is not an accurate indicator of ploidy level (Soltis *et al*., 1992).

The present interpretation is that the original stock was diploid and had been progressively substituted by polyploids. As polyploids often have very slow evolution rates, they may conserve more primitive characters (Stebbins, 1971), as observed in many present day polyploids of Oncidiinae and other groups (Guerra, 2000). This same reasoning is also applied to other primitive and highly polyploid genera of orchids, such as *Neuwiedia* and *Apostasia* (Okada, 1988). On the other hand, diploids and recent polyploids exhibit more derived characters in different parallel evolutionary lines, as *Dipteranthus* in Ornithocephalinae (Williams *et al*., 1994) and *Lockartia* in Oncidiinae (Chase, 1986; Freudenstein and Rasmussen, 1999).

The chromosome analysis of Oncidiinae helps one to understand the seemingly unrelated numbers of the remaining members of tribe Maxillarieae (Table III). Thus, the genera of Lycastinae, Maxillariinae and Stanhopeinae, clearly based on n = 20, may be derived by descending dysploidy from a hexaploid lineage with n = 21. Ornithocephalinae, karyologically known only from two counts in the present work for the genus *Dipteranthus* with 2n = 56 (Figures 3c,d), coincides with the base number of most Oncidiinae genera, supporting its affinity with that subtribe (Chase and Pippen, 1988). Only the subtribe Zygopetalinae seems to be more diversified in the hexaploid-octoploid level (n = 26, 24/48, 23).

The data from Table III suggest the existence of three groups: a larger group (Oncidiinae and Ornithocephalinae), evolved from the base number $x_1 = 7$ and followed by successive cycles of polyploidy and secondary dysploidy; a second group (Lycastinae, Maxillariinae and Stanhopeinae), which is made up of hexaploids with n = 21 that by dysploid reduction led to a secondary base number $x_2 = 20$, and a third group (Zygopetalinae), with a putative base number x_2 = 24 or 26 and no clear relationship with the polyploid series based on $x_1 = 7$. Morphologically, Stanhopeinae and Lycastinae share in common the presence of plicate leaves and elaborated pollination mechanisms (van der Pijl and Dodson, 1966), whereas Oncidiinae and Ornithocephalinae have in common the absence of "sunken glandular trichomes", found in Maxillariinae, Lycastinae and Stanhopeinae (Toscano de Brito, 1998).

In the other tribes of Cymbidioid the best represented chromosome numbers are n = 15, 21 in Malaxideae, n = 14, 21 in Calypsoeae, and n = 27 in Cymbidieae. In Malaxideae, although n = 15 is a very common number, n = 14 has also been found at least in *Liparis* and *Malaxis*. In *Liparis*, the cytotaxonomic interpretation is made difficult by an apparent secondary polyploid series based on x = 10 (n = 10, 20, 40). What is particularly impressive is the high frequency of species with n = 15 in the three genera of Malaxideae, a very rare haploid number in other Cymbidioid (see Table II). Although Malaxideae is the second largest Cymbidioid tribe, it is notably little known, with less than 10% of its species investigated cytologically. In Calypsoeae, n = 14 has only been found in *Calypso*, with n = 21 prevailing in the other genera. If these numbers have a evolutionary history similar to that observed in *Oncidium*, probably they also have or have had representatives with n = 7.

In the tribe Cymbidieae, there is a higher diversity of chromosome numbers, in agreement with the polyphylie observed on the basis of morphological (Freudenstein and Rasmussen, 1999) and molecular evidence (Cameron *et al*., 1999). The main haploid numbers are n = 27 and 23 in the subtribe Eulophiinae, n = 21, 20, n = 28, 27 in the subtribe Cyrtopodiinae, n = 20 in a single species of Acriopsidinae, and n = 27 and n = 34 in Catasetinae. In general the subtribe Eulophiinae is cytologically represented by *Eulophia*, which displays the second largest variation in chromosome numbers known in the phylad. In this genus, a polyploid series based on x = 7 (n = 14, 21, 28, 35, 56) is also represented, with the octoploid level (n = 28, 27) strongly dominant. In *Oeceoclades*, the only two species analyzed are also octoploids, while in *Dipodium* the only record (n = 23) is probably a hexaploid. Poggio *et al*. (1986), analyzing the meiotic behavior of several species of *Eulophia* with n = 21, observed the frequent secondary association of bivalent three-to-three, suggesting that it would be a remaining homeology of the hexaploid condition with x = 7.

In Cyrtopodiinae, the most studied genera are *Cymbidium* with x = 20 and *Cyrtopodium* with x = 23. In the present work original data are supplied for six species of *Cyrtopodium*, one with n = 22 (Figure 1b), four with n = 23 (Figure 1c-e) and one with n = 46 (Figure 1g), reinforcing the importance of x = 23 in the genus. *Cyrtopodium eugenii* with n = 22 is morphologically distinguished from other species of *Cyrtopodium* by the presence of an inflorescence in raceme, whereas others generally present inflorescence in panicle. The numbers n = 28, 27 and 26 are represented in six of ten genera studied of Cyrtopodiinae and n = 21, 20 dominate in another three, once again suggesting a polyploid series with base in x = 7, followed by descending dysploidy. The genus *Cymbidium* is notable for its constancy in chromosome number (n = 20), except the species of subgenus *Jensoa* (*sensu* Christopher and Cribb, 1984), with 2n = 38 (Aoyama and Tanaka, 1988). According to Freudenstein and Rasmussen (1999) *Cymbidium* is a member of the Vandoid phylad while *Jensoa* is part of the large epidendroid polytomy, since *Jensoa* shows later antera bending and lacks other features such as two pollinia or the presence of endocarpic trichomes.

In Catasetinae, of the three cytologically known genera, *Catasetum* and *Mormodes* show x = 27, whereas *Cycnoches* presents x = 34. Of the five species of *Catasetum* studied in the present work, four showed 2n = 54 and one 2n = 108 (Figures 1h,i, and 2a,c), confirming x = 27 for the genus. Although Catasetinae and the genus *Cyrtopodium* display the same pollination syndrome and form a monophyletic group based on cpDNA restriction sites (Chase and Hills, 1992), they are not clearly related karyologically.

As a whole, the great majority of Cymbidioid are ortoploids of the series n = 7, 14, 21, 28 35, 42, 56, 84, or dysploids involving simple reductions. Compared to other large families of angiosperms, such as Poaceae (Hunziker and Stebbins, 1986) or Asteraceae (Watanabe *et al*., 1995), Orchidaceae stands out for the scarcity of representative diploids, where the Cymbidioid phylad is a very good example. These data suggest that the phylad, and consequently the family, may be older than is generally admitted (Garay, 1972), there having been sufficient time for diploids to be widely substituted by polyploids.

Chromosome numbers and habitat variations

In plants, the conquest of new habitats is often related to the occurrence of polyploidy (Stebbins, 1966). Frequently, polyploid races are associated to more extreme environmental conditions (Ehrendorfer, 1970; De Wet, 1986). In the orchid *Anacamptis pyramidalis* (L.) Rich., for example, the polyploid cytotypes are more adapted to regions with geologic formation different from those of diploid populations occurring in the same regions (Del Prete *et al.*, 1991).

Although the orchids constitute a paleopolyploid group (Jones, 1974; Ehrendorfer, 1980), the reversion to terrestrial habitat of typically epiphytic species is apparently acquired more easily when an increase in ploidy level occurs. In the genus *Pleione* (Orchidaceae), for instance, all the epiphytics have 2n = 40 while about 50% of the terrestrial or lithophytic species are higher polyploids (Stergianou, 1989). In the genus *Laelia*, subgenus *Cyrtolaelia*, the lithophytic species are generally allopolyploids (Blumenschein, 1960b). In the present work, a similar tendency was observed. All *Catasetum* and *Oncidium* species, with lithophytic or terrestrial habitats, presented high ploidy levels in comparison with epiphytic species (Table I). In *Oncidium*, *O.* aff. *flexuosum* with 2n = ca. 168 and lithophytic or terrestrial habitat is morphologically closely related to *O. flexuosum* with epiphytic habitat and chromosome number 2n = 56. The same occurs in *O. blanchetii* and *O. varicosum* (2n = 112). Likewise, *Cyrtopodium blanchetii* (2n = 92), with underground pseudobulbs, is tetraploid in relation to the other species with aerial pseudobulbs. Equally, *Catasetum discolor*, with terrestrial habitat, exhibited 2n = ca. 108, while the other species had 2n = 54. On the other hand, the population of *Trigonidium acuminatum* collected in a lithophytic incidental habitat, under strong anthropic pressure, presented the same ploidy level as *T. obtusum* (2n = 40), with epiphytic habitat.

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RESUMO

O clado Cymbidioid apresenta a mais ampla variação cromossômica numérica entre as orquidáceas, com registros desde 2n = 10 em *Psygmorchis pusilla*, até 2n = 168 em duas espécies de *Oncidium*. No presente trabalho, foram estudadas um total de 44 espécies pertencentes a 20 gêneros deste grupo, visando contribuir para esclarecer a evolução cariológica do grupo. Todas as plantas investigadas foram coletadas no Brasil, principalmente na Região Nordeste. A variação cromossômica encontrada foi semelhante àquela previamente registrada na literatura. Os números cromossômicos observados foram: 2n = 54 (subtribo Eulophiinae), 2n = 44, 46 e 92 (subtribo Cyrtopodiinae), 2n = 54, ca. 108 (subtribo Catasetinae), 2n = 52, ca. 96 (subtribo Zygopetalinae), 2n = 40, 80 (subtribo Lycastinae), 2n = 40, 42 (subtribo Maxillariinae), 2n = 40 (subtribo Stanhopeinae), 2n = 56 (subtribo Ornithocephalinae) e 2n = 12, 20, 30, 36, 42, 44, 56, 112, ca. 168 (subtribo Oncidiinae). Os núcleos interfásicos foram bastante variáveis entre os tipos cromocêntrico simples e cromocêntrico complexo, sem aparente valor citotaxonômico. Nos gêneros *Catasetum* e *Oncidium*, as espécies terrestres e rupícolas apresentaram níveis de ploidia superiores àqueles das espécies epifíticas, sugerindo que a poliploidia pode estar envolvida na capacidade de retornar a esse tipo de habitat. O número básico primário x = 7 parece estar associado aos números cromossômicos haplóides da maioria dos grupos de orquídeas Cymbidioid, sendo n = 7 observado apenas em dois gêneros atuais das Oncidiinae. Para cada tribo, subtribo e gênero são discutidos os números básicos prováveis e sua relação com o número básico primário x_1 = 7 admitido para todo o clado.

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