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Chromosome numbers in Begonia[1]

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Summary

The somatic chromosome numbers of 100 Begonia species were counted, of which 72 have been determined for the first time. Eighteen different numbers have been established, ranging between 22 and 156, fifteen of which could be fitted into a tentative scheme of five polyploid series. The most common numbers were 22 (14 species), 28 (35 species) and 56 (17 species).
The species have been grouped into sections according to Irmscher. In some cases these sections appear to have a characteristic chromosome number, while in others, e.g. Pritzelia and Begoniastrum, a great diversity in chromosome number was encountered.

Introduction

The genus Begonia is a very large one, containing more than a thousand species (Irmscher, 1960). Of these about 200 are cultivated and some dozens have at some time or another played a role in the breeding of forms suitable as garden or house plants. The potential of the genus for ornamental horticulture has by no means been exhausted, however. The plants of the present study form part of a collection of over 200 species, which were brought together to be studied for valuable characteristics which might be combined in new hybrid forms.
The possibilities of combining desirable characteristics by hybridization obviously depend on the genetic compatibility of the species and the chromosome number may accordtngly give a first indication of whether or not a cross is likely to succeed. This characteristic is therefore of considerable importance to this project.
For reasons which have been discussed in a previous paper (Doorenbos and Legro, 1969), Begonia chromosomes are hard to count, while literature on the subject is scanty. Until now, the chromosomes of only 46 species have been counted, not all of these counts being conclusive, and in some cases there are even doubts about the identity of the plants.
The present study was started in 1965. The second author collected, grew and identified the plants, the first author did the cytological work. The present paper gives the somatic chromosome numbers of 100 species, 72 of which have been counted for the first time. This means that a little more than half of the species now in cultivation have been investigated, though these constitute only a very small part of this enormous genus, whole sections of which still await cytological study.

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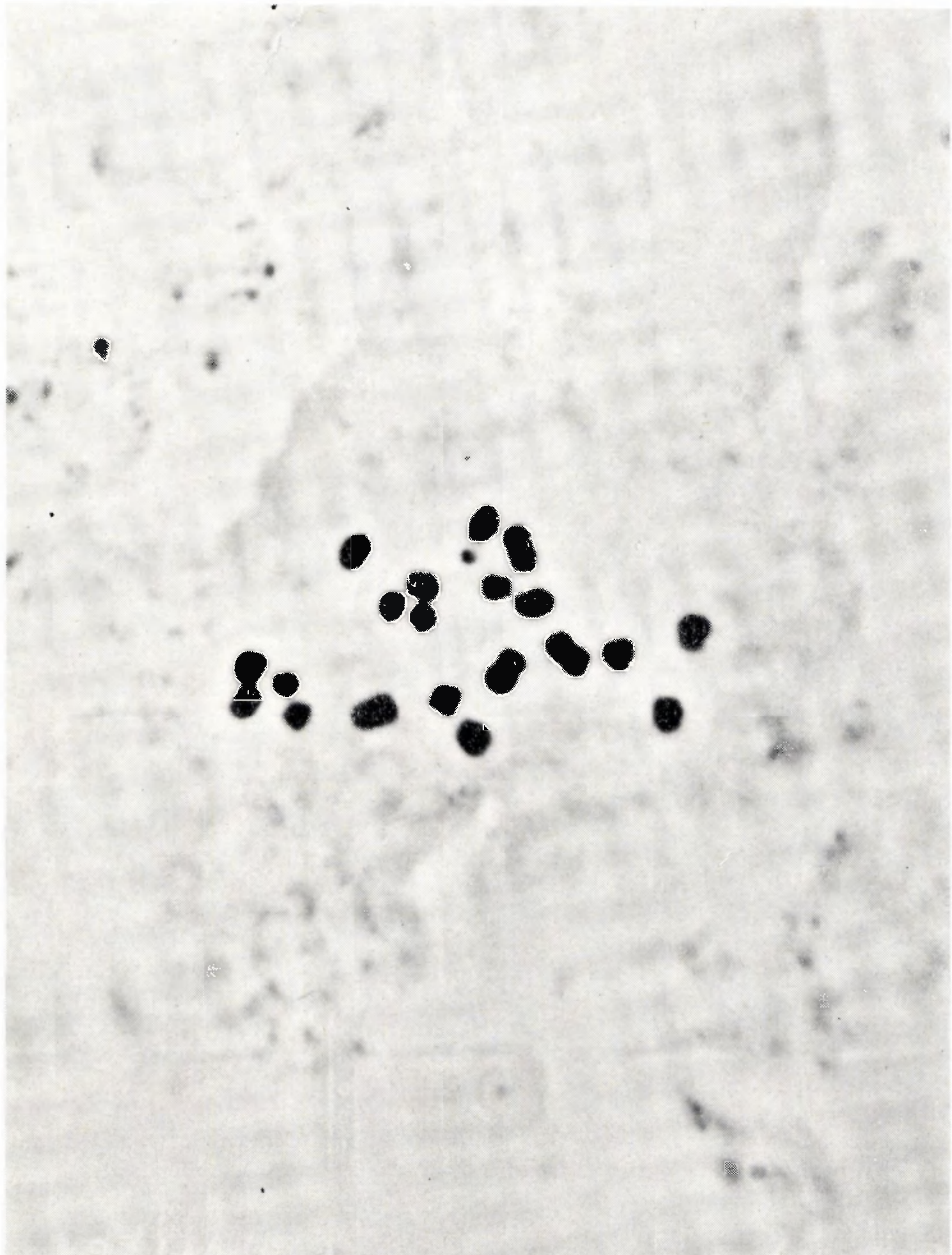

Fig. 1 Begonia cathayana Hemsl. Mitotic metaphase showing 20 chromosomes, one of them having a satellite. The most common number for this species, however, is 22. Enlargement 3800 ×.

Material and methods

The plants used for this study were acquired over a period of 5 years from botanic gardens and private collections, and the present authors are much indebted to the directors and curators of these botanic gardens and to the owners of collections who made their material so readily available. Particularly important contributions were made by the Royal Botanic Gardens in Kew, the Glasgow Botanic Garden and the Royal Botanic Garden in Copenhagen. Many species were obtained from the McKelly Seed Fund of the American Begonia Society.

Some species were obtained directly from the wild, viz *Begonia sutherlandii,* collected by J. J. Bos in Natal, ***B.*** *staudtii* var. *dispersipilosa,* collected by J. J. F. E. de Wilde near Ebolowa in SW Cameroun, *B. eminii,* collected by H. C. D. de Wit near Limbo in Liberia and ***B.*** *acaulis,* collected by J. F. M. Zieck near Rouna in Western Papua. *B. froebelii* was imported from Ecuador, but the exact locality is not known. Some of the seed obtained from the American Begonia Society was also collected in the wild, but no detailed information is available.

The species have been grouped into sections according to Irmscher's review of 1960. This, however, only comprises the species commonly cultivated and in so far as the species of the present study could not be fitted into Irmscher's sections of 1960, his previous and more comprehensive synopsis of 1924 has been used. As Irmscher changed his views in many respects between 1924 and 1960, the use of both classifications may have rise to some inconsistencies.

Considerable attention has been paid to a correct identification of the material. However, the size of the genus and the lack of a comprehensive monograph make the identification of Begonia species a precarious undertaking. The plants have been studied with the help of an extensive collection of Begonia literature. In many cases they have been compared with the original descriptions. Type material has not been consulted. If the correct name could not be found, the species has been omitted.

The chromosome numbers were determined in squash preparations of fresh root tips. They were successively pretreated with a 0.002 M solution of 8-hydroxyquinoline for 4 hours at room temperature and hydrolyzed with 1 N HCl at 60° C. The usual period of hydrolysis of 4–6 minutes proved to be too short for Begonia root tips, while on the other hand a period longer than 10–12 minutes did not improve the staining. Since it was feared that a long hydrolysis might cause chromosome breakage the latter period was adopted.

Of the various staining methods tested, preference was given to the Feulgen technique. The customary time, however, also proved to be too short, a satisfactory result only being obtained after staining for at least 4 hours or overnight. Even then, in the authors' opinion, observation in phase contrast light is indispensable for correct chromosome counting in Begonias.

Microscopes of Carl Zeiss, Oberkochen, were used with, among others, apochromate phase-contrast objectives of 100×/1.32 and wide-angle compensation oculars of 12.5×. In general the counts were verified by two co-operators and at least by one.

Microphotographs were made with a Zeiss 'Vertikal Kamera' on 9 × 12 Gevachrome 32 plates, using phase-contrast light and a green filter. The essential condition for good microphotos of chromosomes in one plane is largely a question of luck, but it was found that this could be improved by a simple technique. The (non-permanent) slide concerned was put on a similar piece of thick ebonite under an old microscope. On the spot of the cell in question a tapered rubber stop was placed onto which

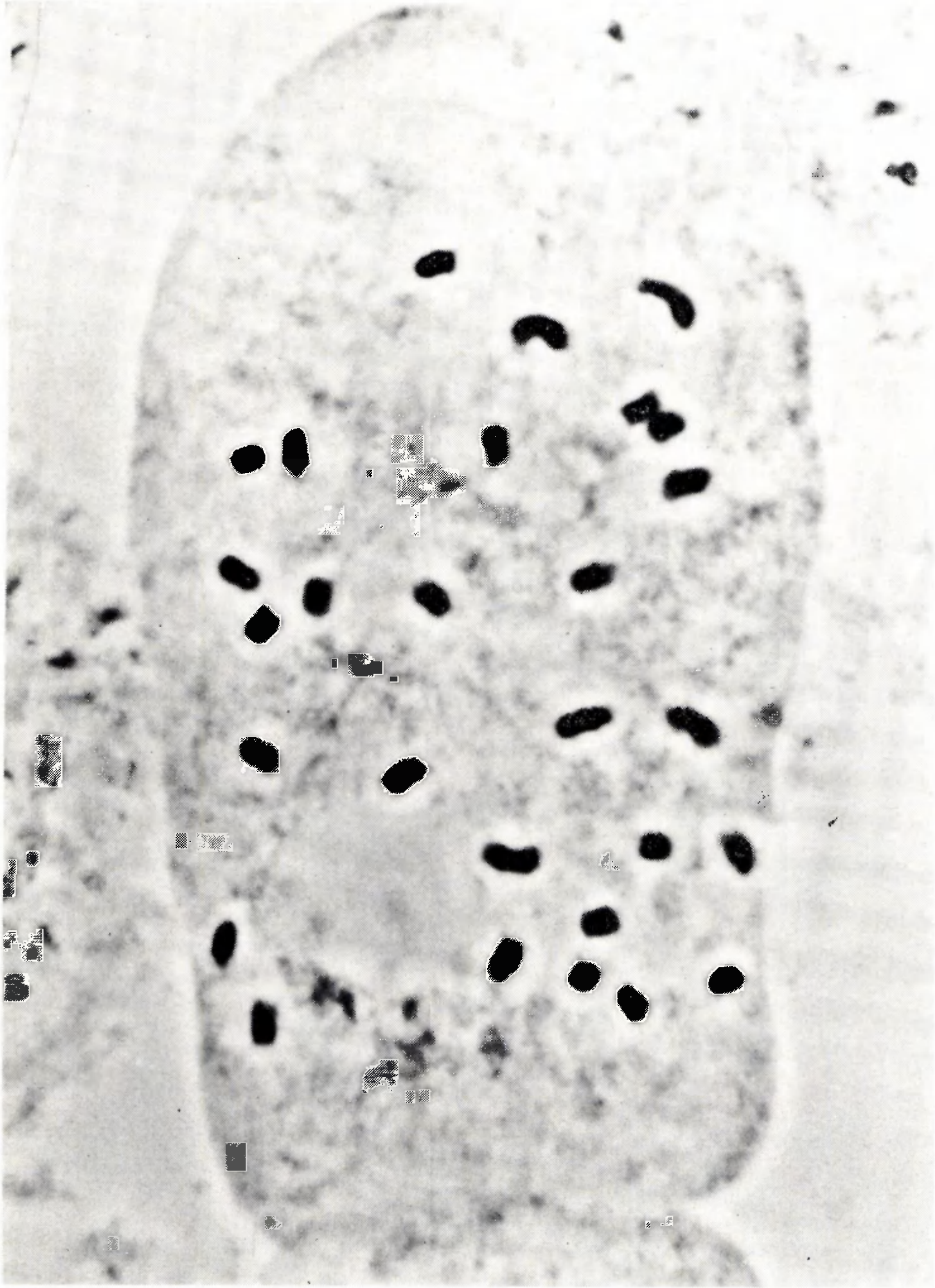

Fig. 2 Begonia boliviensis A. DC. Mitotic metaphase showing 28 chromosomes. Enlargement 3800 ×.

an old objective could be screwed downwards until the slide came under a certain pressure. Dependent on the condition of the cell, a light pressure for about two hours was often sufficient to flatten out the chromosomes, but in extreme cases it took over two days of strong pressure.

Results

In Table 1 the results of the present authors are reported as well as those of previous workers with Begonia species. The chromosome numbers published by Heitz (1927) are omitted because of the high incidence of incorrect results.
In some species it appeared that, apart from clearly determinable chromosomes, one to three stainable fragments were always present too; they have been indicated in the table by +. Their size is about a third of the smallest chromosomes, but whether they are true fragments or very small (or reduced) chromosomes is not clear yet.
Out of a series of microphotographs Fig. 1–5 have been chosen as being the most representative for the wide variation in chromosome number and size.

Table 1 Survey of somatic chromosome numbers in Begonia species in comparison with numbers mentioned by previous authors

		Literature data		
	2n	*2n*	*authors* [1]	*year*
African species				
Augustia				
B. dregei Otto et Dietr.	26	26	M. & O.	1943
B. socotrana Hook. f.	28	28	M. & O.	1943
B. sutherlandii Hook. f.	26			
Scutobegonia				
B. sessilifolia Hook.	38			
B. staudtii Gilg var. dispersipilosa Irmsch.	34			
Tetraphila				
B. eminii Warb.	38			
B. jussiaecarpa Warb.	36+			
B. parva Sprague	36++			
Rostrobegonia				
B. engleri Gilg	26++			
Asiatic species				
Haagea				
B. malabarica Lam.	60	28	S. & B.	1961
Reichenheimia				
B. goegoensis N. E. Br.	34			
Coelocentrum				
B. masoniana Irmsch.	30+++			
Sphenanthera				
B. inflata Grah.	22			
Platycentrum				
B. bowringiana Champ.	22++			
B. cathayana Hemsl.	20, 22			
B. cathcartii Hook. f.	22+			
B. circumlobata Hance	22+			
B. decora Stapf	22			
B. deliciosa Linden	22			

Table 1 (Continued)

		Literature data		
	2n	*2n*	*authors* [1]	*year*
B. diadema Linden	22			
B. hemsleyana Hook.	22			
B. laciniata Roxb.	20, 22	20, 22	S. & B.	1961
B. rubrovenia Hook. f.	22			
B. thomsonii A. DC.	22			
B. xanthina Hook.	22			
Diploclinium				
B. acaulis Merr. et Perry	28			
Petermannia				
B. augustae Irmsch.	44			
B. boisiana Gagnep.	30 ++	30	Piton	1962
B. borneensis A. DC.	30			
B. isoptera Dry.	30	28	Piton	1962
B. serratipetala Irmsch.	44			
Knesebeckia				
B. grandis Dry. var. evansiana (Andr.) Irmsch.	26	26	M. & O.	1943
		24	Bowden	1945
		26	White et al.	1946
		26	O. & N.	1953
B. picta Smith	22	22	White et al.	1946
American species				
Lepsia				
B. foliosa H. B. K.	84	60	Piton	1962
Pritzelia				
B. acetosa Vell.	38+			
B. acida Vell.	38+			
B. coccinea Hook.	56	42	M. & O.	1943
B. convolvulacea A. DC.	38	24	Piton	1962
B. dominicalis A. DC.	56			
B. echinosepala Regel	56			
B. fagifolia Fisch.	38			
B. glabra Aubl. (B. scandens Sweet)	38++			
B. glabra Aubl. var. cordifolia Irmsch.	38			
B. metallica G. Smith	56			
B. parilis Irmsch.	56			
B. reniformis Dry. (B. longipes Hook.)	70	36	Hamel	1937
B. sanguinea Raddi	56			
Trachelocarpus				
B. herbacea Vell.	56			
Gaerdtia				
B. albopicta Bull	56	54	M. & O.	1943
B. corallina Carr.	56			
B. lubbersii Morr.	56			
B. maculata Raddi	56	56	M. & O.	1943
B. teuscheri Linden	56			
B. undulata Schott	56			
Solananthera				
B. limmingheiana Morr.	56			
Barya				
B. boliviensis A. DC.	28			
Tittelbachia				
B. fuchsioides Hook. f.	60	60	M. & O.	1943
Weilbachia				
B. aridicaulis Zies.	28			

Table 1 (Continued)

	2n	Literature data 2n	authors [1]	year
B. imperialis Lem.	28			
B. imperialis Lem. var. smaragdina hort.	28			
B. liebmannii A. DC.	28			
Huszia				
B. cinnabarina Hook.	26			
B. davisii Veitch	28	28	Meyer	1965
B. froebelii A. DC.	28			
B. octopetala l'Hérit.	28	28	Diers	1961
B. pearcei Hook. f.	26			
B. veitchii Hook. f.	28			
Eupetalum				
B. micranthera Griseb.	28			
B. monophylla Pavon	28 (56)			
Giroudia				
B. boweri Zies.	28			
B. boweri Zies. var. nigra-marga hort.	28			
B. carolinaefolia Regel	28			
B. conchaefolia A. Dietr.	28			
B. fusca Liebm.	28+			
B. heracleifolia Cham. et Schlecht.	28+			
B. hydrocotylifolia Otto	28+	24	Hamel	1937
B. involucrata Liebm.	28			
B. kenworthyi Zies.	28			
B. macdougalii Zies.	28			
B. manicata Brogn.	28			
B. maxima A. DC.	28			
B. mazae Zies.	28			
B. nelumbiifolia Cham. et Schlecht.	28			
B. philodendroides Zies.	28+	26	Hamel	1937
B. polygonata Liebm.	28			
B. popenoei Standl.	28			
Donaldia				
B. ulmifolia Willd.	30	30	M. & O.	1943
Saueria				
B. sulcata Scheidw.	72	42	Piton	1962
Begoniastrum				
B. acutifolia Jacq. (B. acuminata Dry)	156	> 100	Piton	1962
B. cubensis Hassk. (B. cubincola A. DC.)	52	36	Piton	1962
B. cucullata Willd.	56	56	Bowden	1945
B. kuhlmannii Brade	48			
B. minor Jacq. (B. nitida Ait.)	78			
B. ottonis Walp.	28			
B. schmidtiana Regel	32++	32	M. & O.	1943
Knesebeckia				
B. dichroa Sprague	56			
B. falciloba Liebm.	28			
B. gracilis H. B. K.	28	84	M. & O.	1943
B. gracilis H. B. K. var. grandiflora Gam.	56			
B. incana Lindl.	28	28	Mereminski	1936
		24	Hamel	1937
B. incarnata Lk et Otto	28	70	Piton	1962
B. olbia Kerch.	56			
B. palmaris A. DC.	28			
B. uruapensis Sessé et Moc.	28			

[1] M. & O. = Matsuura and Okuno, 1943; O. & N. = Okuno and Nagai, 1953; S. & B. = Sharma and Bhattacharyya, 1961.

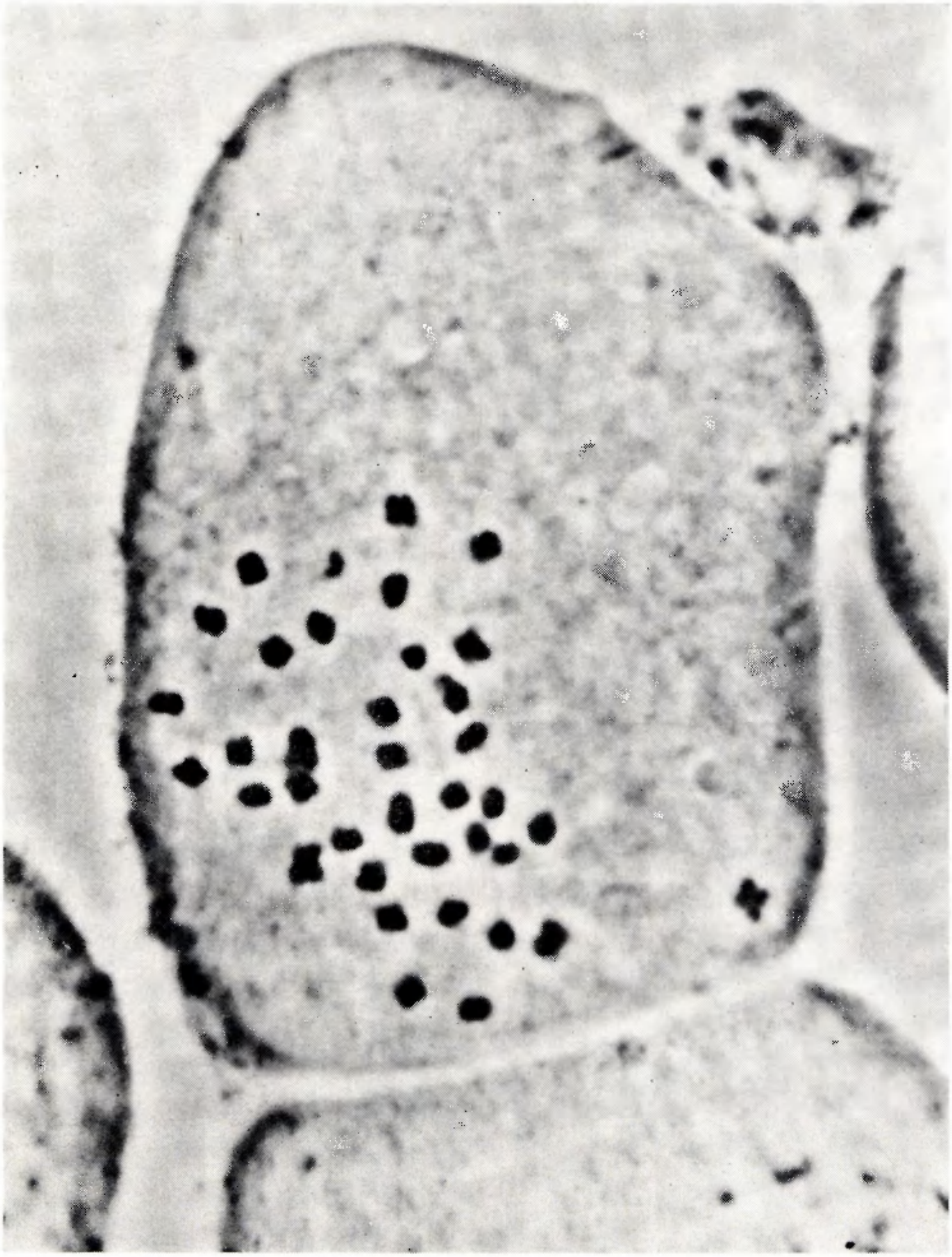

Fig. 3 Begonia jussiaecarpa Warb. Mitotic metaphase showing 36 chromosomes and one fragment (on eleven o'clock). Enlargement 3800 ×.

Discussion

The chromosomes of most species in the present list had never previously been counted, so that comparison of the numbers with those given by previous authors is possible in only 28 cases. Ten of these species had been studied as early 1933–'35 by Matsuura and Okuno (1943). Nevertheless there is complete agreement in 7 cases, and in one case (*B. albopicta*) the difference is only small. Eight species had been studied by Piton (1961) but only in one case the same chromosome number was found.

No less than 18 different chromosome numbers could be established, ranging between 22 and 156. The frequency of the various numbers was very different, however. The most common numbers were 22 (14 species), 26 (6 species), 28 (35 species), 30 (5 species), 38 (7 species) and 56 (17 species). Four numbers were found twice: 34, 36, 44 and 60, and eight numbers occurred only once: 32, 48, 52, 70, 72, 78, 84 and 156.

It may be significant that the number 22 has been found so far only in South Asian species, and 44 only in two species from New Guinea (Table 2). The only numbers of worldwide occurrence appear to be 26 (2 species from America, 3 species from Africa and one from Japan) and 28 (33 species from America, one from the isle of Socotra and one from New Guinea). In American species a wide variety of chromosome numbers were found, although 28 and 56 strongly predominate.

The African Begonias had 26, 28, 34, 36 or 38 chromosomes. The chromosome numbers of South Asian species were 22, 26, 28, 30, 34, 44 or 60. It should of course be kept in mind that only a small percentage of the total number of species have been investigated thus far, and that the genus undoubtedly still has a few surprises in store.

From a closer look at the different sections the following picture emerges. Augustia and the monotypic Rostrobegonia have 26 chromosomes. Only *B. socotrana* has 28, but this species is rather divergent, both morphologically and geographically, from the other species of Augustia.

In the sections Scutobegonia and Tetraphila from West Africa the numbers 34, 36 and 38 appear to predominate. The chromosome numbers of these groups are particularly hard to establish precisely on account of the prevalence of fragments and the generally dense texture of the protoplasm.

According to the present countings, *B. malabarica* from the small section Haagea has 60 chromosomes and indeed it is difficult to understand why Sharma and Bhattacharyya counted only 28. In collections the plant labelled 'Begonia malabarica' is often *B. leptotricha,* which has 28 chromosomes. However, Sharma and Bhattacharyya stated that their plant had pink flowers with two petals which points to *B. malabarica* rather than to *B. leptotricha.*

The large section Platycentrum is apparently characterized by 22 chromosomes. Many

Table 2 Chromosome numbers in Begonia species according to geographic areas of distribution

African species	—	26	28	—	—	34	36	38	—	—	—	—	—	—	—	—	—	—
Asiatic species	22	26	28	30	—	34	—	—	44	—	—	—	60	—	—	—	—	—
American species	—	26	28	30	32	34	—	38	—	48	52	56	60	70	72	78	84	156

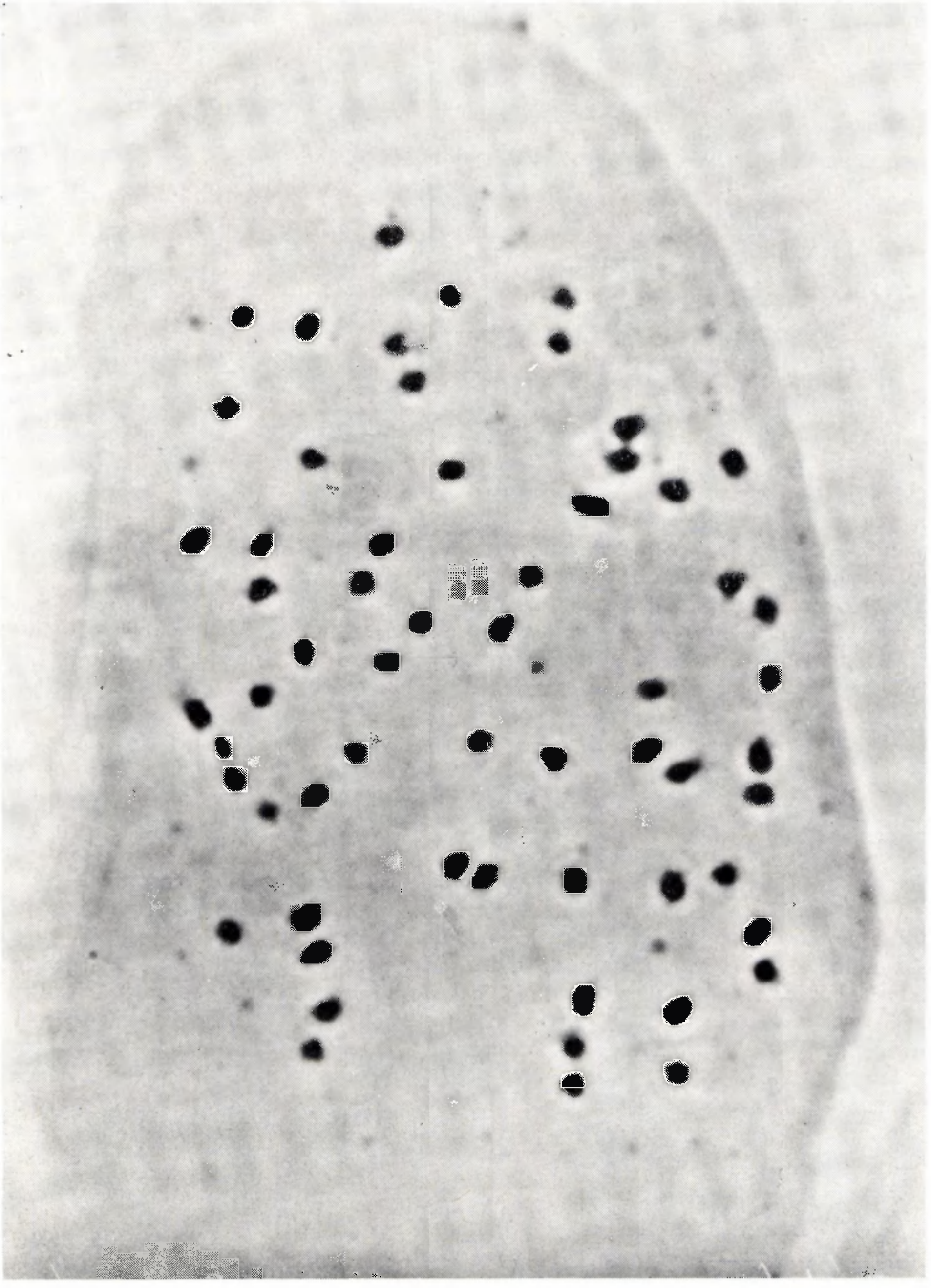

Fig. 4 Begonia malabarica Lam. Mitotic metaphase showing 60 chromosomes. Enlargement 3800 ×.

species of this section are cultivated, the best known being *B. rex* Putz. This has now been hybridized so often that the original form is no longer to be found, or at least not in the collections of the Western world. The present authors could study only hybrids which had 33 or 44 chromosomes. It seems reasonable to suppose that these are polyploids and that the original *B. rex* has 22 chromosomes, a number actually found by Sharma and Bhattacharyya.

Of the species of Petermannia studied, *B. augustia* and *B. serratipetala* occur in New Guinea, while the other three are found much further West (Borneo and Indo China). It may be significant that the former have 44 and the latter 30 chromosomes.

Knesebeckia is a section of American species, to which Irmscher has added *B. grandis* from Japan and *B. picta* from India. Considering the general habit of these plants this seems rather far-fetched and this opinion is confirmed by the chromosome countings, which isolate *B. grandis* and suggest that *B. picta* may be related to the section Platycentrum.

Among the American sections, Pritzelia is a large and heterogeneous one. The predominant chromosome numbers appear to be 38 and 56. The scandent and rhizomatous species studied have 38 chromosomes, while those with 56 are all shrubby. As Alphonse de Candolle has already pointed out, some of the latter (e.g. *B. coccinea*) are very close to Gaerdtia, differing only in the placentae, which are entire in Pritzelia but bifid in Gaerdtia. In this connection it may be of interest that all Gaerdtia species studied also have 56 chromosomes.

The tuberous Begonias of the Andes from the sections Barya and Huszia, which are the ancestors of the modern cultivated tuberous Begonias, have 26 or 28 chromosomes. It should be noted in passing that the two species with 26 chromosomes give fertile hybrids with several of those with 28 chromosomes.

The rhizomatous groups Weilbachia (female flowers with two petals and a two-celled ovary) and Giroudia (female flowers also with two petals, but with a three-celled ovary), although very heterogeneous in leaf form and habit, are cytologically very homogeneous, as all species studied have 28 chromosomes.

Begoniastrum, on the other hand, appears to be very heterogeneous. Some of the species studied have been in cultivation for a very long time (e.g. *B. acutifolia, B. cubensis* and *B. minor*) and the possibility of hybridization should not be excluded. The plants of the three species mentioned which were used for the present study failed to set seed after self-pollination, which is often an indication of a cytogenetic disturbance.

According to the present results, Knesebeckia is cytologically not as diverse as one would expect from the literature. As far as the general morphology of the plant is concerned, however, there is so much variation that one doubts that the last word about this section has been said (*B. dichroa,* for instance, appears to be very close to Gaerdtia, and hybridizes readily with species of this section). It is worthy of note that *B. gracilis* var. *grandiflora* is tetraploid in comparison to *B. gracilis* and the very high chromosome number that Matsuura and Okuna found for this species remains unexplained. Perhaps the plant they studied was a triploid form of *B. gracilis* var. *grandiflora.*

Among the American sections there are a number of small, even monotypic ones. In some cases, these sections appear to be characterized by a divergent chromosome number, e.g. Lepsia, Tittelbachia, Donaldia and Saueria. Others, e.g. Trachelocarpus, Solananthera and Barya, although morphologically distinct (particularly Trachelocarpus, which in its vegetative characteristics hardly resembles a Begonia at all), are

Fig. 5 Begonia acutifolia Jacq. Mitotic metaphase showing 156 chromosomes. Enlargement 1900 ×.

Table 3 Polyploid series in Begonia species in relation to geographic areas of distribution

n	*2n*	*3n*	*4n*	*5n*	*6n*	*12n*	*Provenance*
11	22	—	44	—	—	—	Asia
13	26	38 (39)	52	—	78	156	Africa and America
14	28	—	56	70	84	—	America
15	30	44 (45)	60	—	—	—	America and Asia
16	32	48	—	—	—	—	America

nevertheless in their chromosome number conform to the general pattern of the American species.

In Table 3, a tentative effort has been made to group the chromosome numbers found into five polyploid series. Three numbers, 34, 36 and 72, could not be fitted into this scheme. There are also other reasons to consider this arrangement as a very preliminary one. As the authors have now started an investigation of another hundred species, they intend postponing a more thorough discussion to a later publication.

For a horticultural breeding programme, the present data give valuable indications. A considerable number of crosses have already been made and will be described in further papers. On the whole, crosses are only succesful when the parents have the same number of chromosomes. There are, however, a number of remarkable exceptions, e.g. the succesful crosses between *B. cathayana* (2n = 22) and *B. lubbersii* (2n = 56), between *B. dregei* (2n = 26) and *B. corallina* (2n = 56) and between *B. socotrana* (2n = 28) and *B. sulcata* (2n = 72).

Acknowledgments

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