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REMARKS ON CHROMOSOME NUMBERS IN RUBIACEAE

LEE, YOO SUNG
(Department of Biology, Busan National University, Busan 607, Korea)

꼭두서니科의 染色體數에 對한 系統學的 再考

이 유 성
(부산대학교 문리과대학 생물학과)

Introduction

Although the Rubiaceae is one of the earlist families recognized by many botanists, considerable differences of opinion exist in relation to the taxonomic treatment of this family. The clarification of relationships between related families, and of delimitation of taxa of within this family remains to be completed. It is estimated to be comprised of 6500 species of varying habits (mostly shrubs and trees) occupying an array of habitats.

The vegetative and floral diversity in the family has resulted in the arrangement of diverse groupings. In spite of the classification difficulties the family is characterized by the followings: inferior ovary; regular or nearly regular corolla; stamens as many as and alternate with corolla lobes; opposite leaves with interpetiolar stipules, or whorled leaves without stipules; and nuclear endosperm.

The Rubiaceae as considered by Cronquist (1968) is a somewhat aberrant family, in which the evaluation of multi-disciplinary data will likely bring many changes. Earlier, the order Rubiales (of both Bessey and Engler, Rubicinae of Hallier) was composed of Rubiaceae, Adoxaceae, Valerianaceae, Caprifoliaceae, and Dipsacaceae. Bentham and Hooker (1862-83) retained only the Caprifoliaceae including Adoxaceae, and Rubiaceae in the Rubiales and transferred the rest to the Asterales. Hutchinson (1959) retained only the Rubiaceae in the Rubiales and transferred the Caprifoliaceae to the Araliales (Archechlamydeae), Adoxaceae to Saxifragales, Valerianaceae and Dipsacaceae to Valerianales.

More recently Wagenitz (1959) indicated that the order Rubiales as defined in Engler's Syllabus cannot be regarded as natural. Because, the similarities between the Rubiaceae and the other families included in this order appear to be less important than those between the Rubiaceae and some of the families that were included in the order designated Contortae. Wagenitz (1959), Thorne (1968) and Takhtajan (1969) transferred the Rubiaceae to the order Gentianales, and indicated a relationship to

the family Loganiaceae. The other families, of the former Rubiales, are maintained in the order Dipsacales as described by Lindley (emended by Nakai). Cronquist (1968) considered it useful to maintain the single family Rubiaceae in the Rubiales.

Although relatively little is known cytologically, compared to the size and economic importance of the family, a reasonable amount data have accumulated in the last 35 years. Fagerland published a comprehensive report in 1939 which allowed him to determinate chromosomal interrelationships and phylogenetic consideration of the family. Chromosome information has been used to indicate some unsuspected relationships and/or endored some existing opinions concerning possible affinities. Many gaps presently exist in the chromosomal knowledge, and some interpretations may be changed as additioned cytological data accumulate. Nevertheless, it should be indicated that chromosomal information would be one of the important aspects to better understanding this family.

In this publication, the base haploid number, polyploidy, distribution, ancestry and evolution regarding chromosome number will be discussed.

Materials and Methods

Chromosome data were compiled for the family Rubiaceae from the literature. Two main references for the chromosome numbers in the Rubiaceae and its related families were the Chromosome Numbers of Flowering Plants written in Russian by Z. Bolkhovskikh et al (1966) and Index To Plant Chromosome Number 1967-71 by R.J. Moore (1973). Some of earlier and apparently erroneous counts have been omitted.

The arrangement of genera into tribes follows Wagenitz.

The related families were arranged following Takhtajan's Classificaion (1969). Data on geographic distribution has been compiled mainly from Wagenitz, Verdcourt (1959) and specimens in the New York Botanical Garden Herbarium.

Results and Discussions

The Rubiaceae like most of the large dicotyledonous fmilies have received comparatively little cytological attention. The chromosome number of approximately 730 species are known which is little more than ten per cent of the whole family. Nevertheless, taxa from apparently all the grouping have been counted. Thus this permits some reasonable consideration regarding the base number, polyploidy, distribution, inter/intra-relationship, ancestry and evolution of the family.

A spectrum of chromosome numbers is known to exist in the family between the lowest 2n=12 (*Hedyotis nutalliana* Fosb., *H. watsonii* Lewis), and highest 2n=220 (*Coprosma ernodeoides* A. Gray, *Galium grande* McClatchie). Other taxa with very high numbers are: *Coprosma pumila* Hook *f.* (2n=154), *Galium ovata* (Wawra) Skottsb. (2n=102, 104), *G. palustre* L. var. *aparinoides* Neum (2n=100), *Kadua centranthoides* Hook et Arn. (2n=100), and *Galium elongatum* Presl. (2n=96).

The base numbers of the genera in the family reveal the presence of 6 through 14 and 17 series.

The predominant base number in the family is x=11 (2, 3, 6, 8, 10, 12, 14, 20x) followed by x=9 (4, 6, 8x) (Fig.1). A majority of the known chromosome numbers from diverse tribes have a base number of x=11. A high degree of morphological differentiation has taken place in the family without a large number of changes in chromosome numbers (Stebbins, 1950). The base number x=9 could be of independent origin or secondarily derived from x=11. It is possible that those close to base number x=11 might have been derived by aneuploidy, with addition (x=12) such as *Catesbaea latifolia* Lindbl., or reduction (x=10) such as *Asperula molluginoides* Reichenb.

Some authors have indicated the possible relationships of the Rubiaceae with other families. Apart from the morphological similarities, researchers should determine families which have genera predominantly based on x=11 and its derivatives.

The Rubiaceae seemingly form a connecting link between the Gentianales and Dipsacales, and yet they would be an abnormal element in either order (Cronquist, 1968). The characteristics of the groups have been discussed by Wagenitz (1959), who concluded that the Rubiaceae should be included in the Gentianales, and the resemblance of the Rubiaceae to Caprifoliaceae (Dipsacales) is the result of convergence rether than indication of close relationship. The evidence from considering its predominant base chromosome numbers (Table 2) supports Wagenitz's opinion. In the Gentianales (Table 2), the Rubiaceae is more similar to the Apocynaceae, Asclepiadaceae and Loganiaceae than the Gentianaceae and Menyanthaceae. The families of the Dipsacales are less similar to the Rubiaceae in the base numbers, although the family Dipsacaceae might be considered be close. It is possible that the Gentianales had a common origin, from the Saxifragales, with Cornales and Dipsacales as suggested by Takhtajan (1969). Considering base number, the Gentianales is similar to the Cornales (Table 2, Fig. 2). But the possible determination of the Gentianales from the Saxifragales is not clear. Bentham and Hooker's (1876) and Bensen's (1957) placement of Rubiaceae together with the familes of Dipsacales in order Rubiales is not supported by the evidence obtained from the base chromosome numbers. The Rubiaceae of Gentianales as treated by Takhtajan (1969) seems to more accurately reflect the chromosome data since the majority of families are x=11.

It should be noted again that a discussion about relationships should not only include base chromosome numbers for good conclusion.

Approximately 30–35 per cent of the species of the flowering plants are polyploids (Stebbins, 1971). The known taxa of the Rubiaceae reveal approximate 40% polyploidy. The number of polyploid species with different base numbers is presented in Table 3. The obtained percentages may reflect a bias because not enough species has been examined except for x=11. The polyploid series of x=11 reveal a wide range of repeated polyploidy, from triploidy to 20-ploidy: *Ixora rosea* Wall. (3-ploid), *Nertera scapanioides* Lange (4-ploid), *Galium boreale* L. (5-ploid), *Rubia peregrina* L. (6-ploid), *Myrmecodia echinata* Gaudich (8-ploid), *Galium anisophyllum* Vill (10-ploid), *Rubia peregrina* L. (12-ploid), *Coprosma pumila* Hook *f.* (14-ploid), and *Coprosma ernodeoides* A. Gray (20-ploid).

Polyploidy has been much compounded in tribes as Hedyotideae, Ixoreae and Rubieae, and probably most often has been associated with hybridization. It is believed that both polyploidy and aneuploidy in the x=11 series seem to have been particularly effective in speciation. It is also noticeable that

the most advanced family characteristics can be found in taxa with repeated polyploidy of x=11.

A few epiphytes in the tribe Psychotrieae (*Hydnophytum, Myrmecodia* etc.) are considered advanced species. Scandent plants occur in the tribes: Ixoreae, Naucleae, Paederieae (mostly) and Vanguerieae. Unisexual flowers occur in a few Gardenieae, very few Rubieae (some *Asperula*) and many Anthospermeae. Only taxa from one tribe, the Guettardeae have seeds without endosperm. Aggregate fruits are found in *Morinda* and some Naucleae. Dry fruits occur in a large number of genera (Verdcourt, 1958). These examples indicated above occur in only the x=11 series. which is considered to be an actively developing group in the Rubiaceae. The occurence of the base number of x=11 in many large and diverse tribes also suggest a complement of some antiquity (Lewis, 1962) (Table 1).

In the chromosome number distribution in the family, the diploid numbers in Group A with the base number of x=9, 10, 11, and 12 reappeared in Group B after the chromosome doubling through probably natural hybridization. The Group B likely resulted from tetraploidy of the same base numbers.

2n	12	14	16	18	20	22	24	26	28	32	33	34	36	40	44	48	54	56
No.of sp.:	5	1	3	38	15	293	15	6	15	6	1	5	36	14	155	15	2	4
				A									B					

66	68	72	84	88	96	100	110	132	154	220	AN*	Total
24	3	10	4	13	5	1	1	2	1	3	36	730

Phytogeography sometimes provides information which helps delineate groupings. The geographical distribution of 69 genera with different base numbers are presented in Table 4. The family has a wide distribution and this probably indicates a very ancient family. With a predominant pantropical distribution in the modern flora, there is little doubt that the Rubiaceae had their major evolution in the tropics; possibly beginning in the Triassic or Jaurassic followed by the exploitation of some extra-tropical environment in the Cretaceous (Axelrod, 1960). Verdcourt (1958) indicated chromosome counts would be of little assistance in classification of taxa in tribes, The tribes widespread throughout the tropics, such as Psychotrieae, Morindeae, Guettardeae, Gardenieae, Ixoreae and Paederieae have a x=11 base number only. The tropical tribes widely distributed but not in Austrialia, such as Mussaendeae and Cinchoneae have a base number of x=9 through 13 or 17. The tribes occurring in both the tropics and temperate regions, such as Hedyotideae, Spermacoceae, Anthospermeae and Rubieae reveal a diverse base number x=7 through 13 or 14.

Tropical tribes not represented in Africa, such as Rondeletieae and Chiocceae have a base number of x=11 or 12; the one not represented in South America, such as *Ophiorrhiza, Urophyllm* and Knoxieae x=9, 10 or 11. In the Rubiaceae, or at least some groups of them, the idea that the base chromonosome number and georgraphical distribution are correlated may be valuable on the assumption since many tribes having only x=11 remain the tropics, and the tribes having diversed base numbers have spread to a wider geographical distribution. It seems possible when consideration is given to diverse characters that the tropical tribes having only x=11 are the oldest.

Rubieae is a tribe with apolyploid series of x=11 which has been successful in many geographical area. Many of the Rubieae have a large number of different fruit types, which indicate many disposal

adaptations such as: the pericarp being dry or flesh, their surface being covered with hooked or straight hairs. papillae, or wings, or sooth. In derived groups the modification of pedicels, peduncles and bracts had led to elaborate complex dispersal structures.

Polyploids usually have different geographic distributions from their diploid ancesters, and are likely to be particuarly frequent and diverse in regions newly opened to colonization (Stebbins, 1950). Polyploid elements of the strictly annual and predominantly autogamous *Galium aparine* complex are among the most successful colonizing weeds of flowering plants and accompanied man to may parts of the world. This complex originated by allopoliploidy (2, 4, 6, 8, 10x) from basic diploids with structural and dysploid differentation of genomes (x=11 and 10) (Ehrendoreer, 1965).

As many researchers have found, the chromosome numbers of a species can not be doubled indefinitely without deleterious results (Stebbins, 1950). For each species, there seems to be an optimum chromosome number, which may be diploid, tetraploid, or hexaploid, but rarely as high as those in Hedyotideae and Rubieae.

It seems apparant that additional study of the chromosomes combined with other available data would be possible to better determine the inter/intra-relationships.

摘 要

Rubiaceae(꼭두서니과) 식물의 염색체수를 문헌조사에 의하여 재정리 분석하고, 科내외의 유연관계, 조상, 진화, 분포, 배수체, 기본염색체수 등을 논의하였다.

이 科에 속하는 식물중 약 730종(>10%)의 염색체수가 현재 알려져 있으며 최저 2n=12부터 최고 2n=220까지 달한다. 기본염색체수는 "6"~"14", 그리고 "17"계열로 존재하며, 가장 빈도높게 나타나는 숫자는 X=11 (2, 3, 6, 8, 10, 12, 14, 20X)이고 그 다음이 X=9(4, 6, 8X)이다.

고도의 형태적 분화도 염색체의 큰 변화없이 이루워졌다. 빈도 높은 기본염색체수는 Wagenitz의 분류체계를 지지한다. 즉 Gentianales에 있어서 Rubiaceae는 Gentiancaeae, Menyanthaceae보다 Apocynaceae, Asclepiadaceae, Loganiaceae와 더욱 근친성을 갖는다. 또한 Rubiaceae는 Dipsacales에 속하는 여러 科와는 근친성이 비교적 낮다. Gentianales, Cornales는 서로 가깝지만 이들이 공통 조상인 Saxifragales에서 유래되었는지는 기본염색체수로서 분명치 않다.

Rubiaceae는 약 40%가 배수체현상을 나타냈다. X=11계열의 배수체현상은 3배체부터 20배체까지 광범위하게 중복해서 나타냈다. 이 계열의 polyploidy와 aneuploidy는 종의 분화에 많은 영향을 미치고 있다고 생각된다. 가장 진보적인 科의 특징들은 X=11의 반복된 배수체현상을 가진 taxa에서 발견되는 것은 주목할만하다.

Rubiaceae에 있어서는 기본염색체와 지리적 분포는 상관관계가 있다. X=11만 가진 여러 tribes (族)들은 열대에 남아있는데 반해, 여러 갈래의 기본염색체수를 가진 族들은 보다 광범위한 지리적 분포를 보여주었다. X=11만 가진 族들이 가장 오래된 것으로 생각된다. Tribe Rubieae는 X=11계열의 배수체들을 가진 族으로서 여러 지리적 분포에서 성공적이었다.

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Table 1. Distribution of chromosome numbers in tribes of Rubiaceae

Tribes	12	14	16	18	20	22	24	26	28	32	33	34	36	40	44	48	54	56	66	68	72	84	88	96	100	110	132	154	220	An*	Total
Anthospermeae						8				1				1	12				1									1	1	2	27
Chiococceae							1								1																2
Cinchoneae						2		1				3	6	3						3	6								1		25
Gardenieae						20						2																		2	24
Guettardeae															2																2
Hamelieae							3									5															8
Hedyotideae	5	1	3	25	8	13	3	5	2	5			17	1	1	2	2				3									4	99
Ixoreae						55					1				11				2				1							2	72
Knoxieae					1									6																	7
Morindeae						2																									2
Mussaendeae				2		9							2		1															1	15
Naucleae						1									4																5
Paederieae															1																1
Psychotrieae						23									8								1								32
Rondeletieae						3									2															3	8
Rubieae				4		122	8								96	3			20				11	5	1	1	2		1	22	296
Spermacoceae						1			13						1			4				4								1	24
Vanguerieae															5																5
Unknown				7	6	34							11	3	10				1		1									3	76
(Total)	5	1	3	38	15	293	15	6	15	6	1	5	36	14	155	10	2	4	24	3	10	4	13	5	1	1	2	1	3	39	730

*Aneuploidy

Table 2. Predominant base chromosome numbers in major families of Gentianales, Dipsacales, Cornales and Saxifragales

Gentianales:		Cornales:	
Apocynaceae	x=10, 11	Cornaceae	x=8, 9, 11
Asclepiadaceae	11	Garryaceae	11
Gentianaceae	9, 10, 13	Nyssaceae	11
Loganiaceae	10, 11	Araliaceae	12
Menyanthaceae	27	Apiaceae	8, 11
Rubiaceae	9, 11	Saxifragales:	
Dipsacales:		Cunoniaceae	12, 15, 16
Adoxaceae	9	Iteaceae	11
Caprifoliaceae	9	Buxiaceae	8
Dipsacaceae	8, 9, 10	Grossulariaceae	8
Valerianaceae	7, 8	Hydrageaceae	9
		Pittosporaceae	12
		Bruniaceae	8
		Crassulaceae	9, 17
		Saxifragaceae	12, 13, 14
		Parnassiaceae	9

* The underlined numbers are the most frequent one.

Table 3. Number of polypoid species of Rubiaceae with different base chromosome numbers.

x:	Total species	Polyploid species	% of polyploid.
6	5	0	0.0
7	16	8(4, 8, 12x)	50.0
8	9	6(4x)	66.7
9	84	47(4, 6, 8x)	56.0
10	30	15(4, 10x)	50.0
11	493	200(3, 4, 6, 8, 10, 12, 14, 20x)	40.6
12	30	15(0)	50.0
13	6	0	0.0
14	8	0	0.0
17	8	3(0)	37.5
AN*	41	—	—
Total	730	294(4-20)	40.2

* aneuploidy

Table 4. Georaphical distribution of the selected 69 genera of Rubiaceae according to the base chromosome number.

x:	Tropical Africa	South Africa	Europe	Tropical & Subtropical Asia	Australia	Oceania	South America	Central & Tropical America	Total:
6	2 (1)	—	—	2 (1)	—	—	—	2 (1)	6 (3)
7	6 (5)	2 (2)	—	3 (2)	—	—	2 (1)	6 (4)	19(14)
8	3 (1)	—	—	2 (1)	—	—	—	2 (1)	7 (3)
9	10 (5)	1 (0)	1 (0)	5 (3)	—	—	1 (1)	8 (7)	26(16)

10	3 (2)	2 (2)	—	3 (2)	3 (3)	2 (2)	2 (2)	3 (2)	18(15)
11	27(12)	10 (4)	6 (4)	33(17)	8 (6)	5 (3)	12 (9)	18(10)	119(65)
12	2 (1)	1 (1)	—	2 (0)	—	—	2 (1)	3 (0)	10 (3)
13	—	—	—	—	—	—	1 (0)	1 (0)	2 (0)
14	1 (0)	—	—	1 (0)	—	—	—	—	2 (0)
17	—	—	—	1 (1)	—	—	—	2 (1)	3 (1)
Tot.	54(27)	16 (9)	7 (4)	52(27)	11 (9)	7 (5)	20(14)	45(26)	212(121)

* The number in parentheses indicates polyploid genera.
* 69 genera were selected from both well known distribution data and chromosome numbers.
* Genera including more than one category in either geographical distribution or chromosome numbers are considered duplicately as much as they are frequent.

Table 5. Distribution of the base chromosome number in tribes of Rubiaceae.

Anthospermeae	8(4x), 10(4x), 11(2, 4, 6, 14, 20x)
Chiococceae	11(4x), 12(2x)
Cinchoneae	9(4, 8x), 10(4x), 11(2x), 13(2x), 17(2, 4x)
Gardenieae	11(2x), 17(2x)
Guettardeae	11(4x)
Hamelieae	12(2, 4x)
Hedyotideae	6(2x), 7(2x), 8(2, 4x), 9(2, 4, 6, 8x), 11(2, 4x), 12(2, 4x), 13(2x), 14(2x)
Ixoreae	11(2, 3, 4, 6, 8x)
Knoxieae	10(2, 4x)
Morindeae	11(2x)
Mussaendeae	9(2, 4x), 11(2, 4x)
Naucleae	11(2, 4x)
Paederieae	11(4x)
Psychotrieae	11(2, 4, 8x)
Rondeletieae	11(2, 4x)
Rubieae	9(2x), 10(10x), 11(2, 4, 6, 8, 10, 12, 20x)
Spermacoceae	7(8, 12x), 11(2, 4x), 14(2x)
Vanguerieae	11(4x)
Unknown	9(2, 4, 8x), 10(2, 4x), 11(2, 4, 6x)

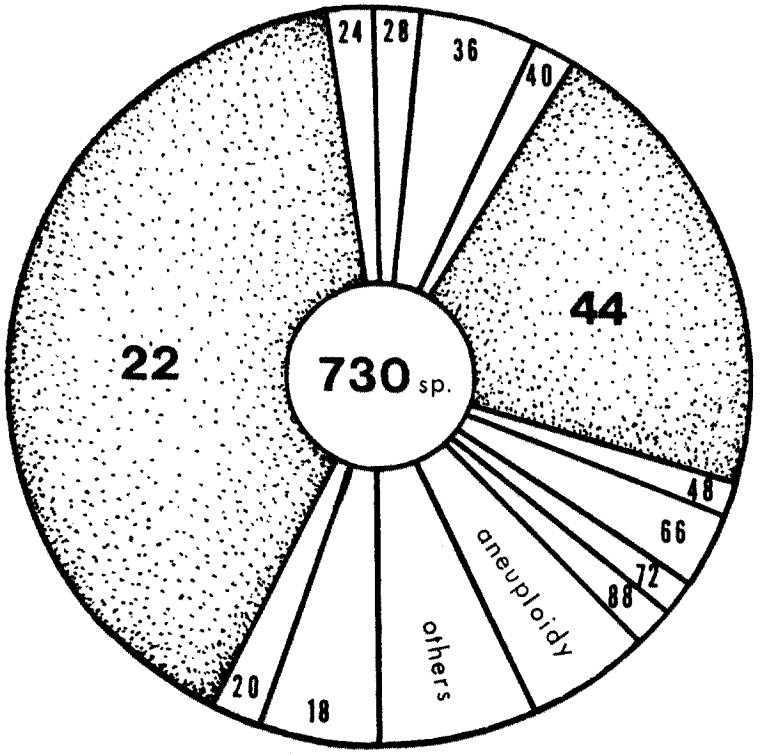

Fig. 1. Ratio ot the chromosome number distributed in the Rubiaceae.

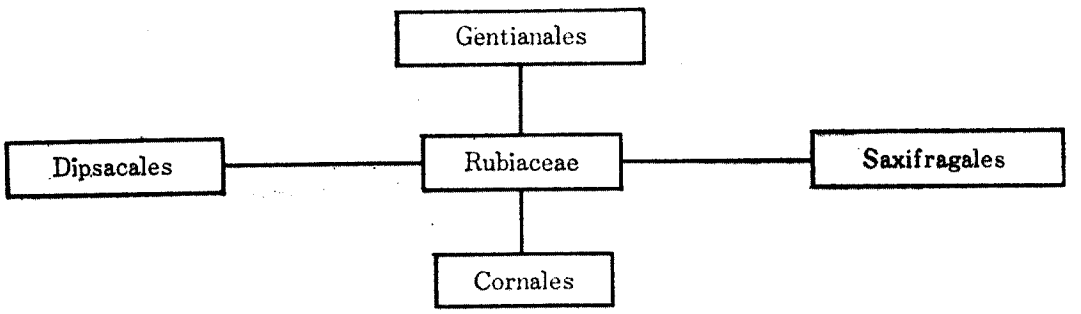

Fig. 2. Relative distance to the Rubiaceae according to the base chromosome number.