

THE BASES OF ANGIOSPERM PHYLOGENY: CYTOLOGY¹

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ABSTRACT

A broad review of chromosome numbers in the angiosperms is presented according to the phylogenetic system of Cronquist. Consideration of the results indicates that the original basic chromosome number for the class as a whole, and for all but one of its subclasses, is or may well be $x = 7$. For Caryophyllidae, $x = 9$ is indicated. Families and taxa of higher rank can be compared only if the original basic chromosome number for the group is known, and there are many families where this is not the case. Evolutionary changes in chromosome number and morphology, particularly in herbaceous plants, have tended to give the impression that these characteristics were of limited utility in classification, and have often led to numerical coincidences between unrelated groups. In addition, many inaccurate counts have been reported, and vouchers, if present, are occasionally misidentified, giving rise to misleading conclusions. Electronic data processing should be applied to the field as soon as possible for efficient information retrieval, especially since the number of chromosome counts reported is growing annually. Well edited regional treatments, or those dealing with a particular taxonomic group, are encouraged. An initial burst of polyploidy is suggested for the angiosperms by the survival of many polyploid lines, especially among Magnoliidae and Hamamelididae. Although many families and even orders are of polyploid origin, progressive evolution in the group seems to have proceeded largely at the diploid level, and much of the major differentiation evidently occurred even among plants with the original basic chromosome number, $n = 7$.

For more than 50 years, chromosome cytology has been an important element in evaluating relationships and deducing phylogenetic sequences in the angiosperms. Data derived from this field are potentially useful, especially in woody plant groups (Darlington & Mather, 1949; Darlington, 1956), but the use of such data is not simple, as will be illustrated in the following pages. Changes in chromosome number and morphology may be rapid even within a genus (Stebbins, 1966), a tendency that had made many students of phylogeny mistrust or downgrade the importance of chromosomal information for broad considerations. Insufficient information, inaccurate information, and the necessity of understanding the pattern in one taxon before it can be compared on this basis with another taxon all contribute to the difficulty of using such information in systematic or evolutionary studies.

MATERIALS AND METHODS

The principal sources of information on the chromosome numbers of angiosperms are the compendia of Darlington & Janaki Ammal (1945), Darlington &

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Wylie (1955), and Bolkhovskikh et al. (1969). In addition, there is the annual *Index to Plant Chromosome Numbers*, the most recent number of which summarizes reports for 1972 (Moore, 1974). Some measure of the interest in chromosome cytology may be deduced from the fact that whereas counts for 1821 genera were summarized in 1945, there were 2693 by 1955 and 4679 by 1969 (including reports up to 1966). Electronic data processing could be applied very profitably to this field, and it ought in principle to be possible to add successive counts to a data bank which could be queried at any time for any taxon of interest. Editing is however a very serious problem; in the list of Bolkhovskikh et al. (1969) the same species are often listed under two or more generic names. With the changing limits of families, it is often no simple matter to know where to look for a given genus. Closely edited regional compendia such as that of Löve & Löve (1961) are likely to be most useful, but few people have the knowledge to edit a world chromosome list to this level. We shall probably see more and more regional treatments and treatments of particular taxa, such as families, in which the editing can reach a high standard.

A considerable and totally unnecessary element of confusion is introduced into all phylogenetic considerations by the fact that the *International Code of Botanical Nomenclature* limits the principle of priority to taxa of the rank of family and below. Thorne (1968, 1974) has used the principle of priority in determining the names of orders, while Cronquist (1968) and Takhtajan (1969) have not. There seems to be no advantage to anyone in arbitrarily using two or more names for the same order, and the simplest way to solve the problem, now that general agreement is becoming apparent on the limits of many orders, would be to apply the principle of priority to taxa at this rank also.

Even when the problems of information retrieval and editing of the data have been overcome, however, there remain a series of other difficulties. Reports of chromosome numbers prior to World War II were rarely associated with particular voucher specimens, and the identity of the plants cannot then be verified. Inaccurate counts are fairly frequent, especially in papers which contain listings for many families. All reports prior to 1920 were made from sectioned material, the interpretation of which presents special difficulties. In preparing the summary statements for various taxa in this paper, I have simply disregarded a number of counts which have not been verified or were included in papers suspected to contain a high proportion of erroneous counts.

It is of the utmost importance in the application of chromosomal information at the family level first to deduce the original basic chromosome number of the taxon in question. The bulk of this paper is devoted to a consideration of such hypotheses, since without knowing the original basic chromosome number of a family or other taxon, it is not possible directly to compare it with any other. Similar considerations have been pointed out by Thorne (1963), Cronquist (1968), and many others for deducing phylogenies in general; but numerical coincidence is so great that the matter becomes a particularly important one with respect to chromosome number.

RESULTS

GAPS IN THE RECORD

Of the 354 families recognized by Cronquist (1968), there are 44 for which no cytological information is available at present. They are listed with the number of genera and species and their ranges from Airy Shaw (1966):

Achariaceae (3/3, South Africa), Aextoxicaceae (1/1, Chile), Akaniaceae (1/1, eastern Australia), Alseuosmiaceae (3/11, New Caledonia, New Zealand), Ancistrocladaceae (1/20, Old World tropics), Balanopaceae (1/12, Australasia), Barbeyaceae (1/1, northeastern Africa, Arabia), Cardiopterygaceae (1/3, southeastern Asia, Australia), Caryocaraceae (2/25, tropical America), Cephalotaceae (1/1, Western Australia), Columelliaceae (1/4, South America), Corsiaceae (2/10, New Guinea, Chile), Dialypetalanthaceae (1/1, tropical America), Didymelaceae (1/2, Madagascar), Dipentodontaceae (1/1, temperate Asia), Ecdeiocoleaceae (1/1, Western Australia), Geissolomataceae (1/1, South Africa), Geosiridaceae (1/1, Madagascar), Grubbiaceae (2/3, South Africa), Hoplestigmataceae (1/2, tropical Africa), Hydnoraceae (2/18, South America, Africa), Julianiaceae (2/5, tropical America), Lissocarpaceae (1/2, tropical South America), Marcgraviaceae (5/100, tropical America), Mayacaceae (1/10, tropical America and Africa), Medusagynaceae (1/1, Seychelles), Medusandraceae (1/1, tropical Africa), Myrothamnaceae (1/2, Africa), Myzodendraceae (1/11, South America), Pentaphragmataceae (1/30, tropical Asia), Peridiscaceae (2/2, South America), Petrosaviaceae (1/3, tropical Asia), Picrodendraceae (1/3, West Indies), Quiinaceae (4/50, tropical South America), Rhoipteleaceae (1/1, southeastern Asia), Sarcolaenaceae (8/33, Madagascar), Siphonodontaceae (1/5, southeastern Asia, Australia), Stylobasiaceae (1/2, southwestern Australia), Thurniaceae (1/3, tropical South America), Tovariaceae (1/2, America), Tremandraceae (3/25, Australia), Trigoniaceae (4/35, tropical), Vochysiaceae (6/200, tropical America and Africa), and Xanthophyllaceae (1/60, tropical Asia).

Of the additional families recognized by Thorne (1968) and by Takhtajan (1969), there is no cytological information available for the following 49: Anisophylleaceae (4/36, tropical), Asteropeiaceae (1/7, Madagascar), Balanitaceae (1/25, Old World tropics), Biebersteiniaceae (1/5, Eurasia), Bonnetiaceae (3/22, tropical Asia and America), Bretschneideraceae (1/1, southwestern China), Brunelliaceae (1/45, tropical America), Diegodendraceae (1/1, Madagascar), Dirachmaceae (1/1, Socotra), Donatiaceae (1/2, subantarctic), Emblingiaceae (1/1, Australia), Eremosynaceae (1/1, Australia), Erythraliaceae (1/2, Indomalaysia), Goupiaceae (1/3, tropical South America), Halophytaceae (1/1, southern South America), Hanguanaceae (1/2, Ceylon, Malaysia), Hectorellaceae (1/1, New Zealand), Huaceae (1/2, tropical Africa), Hypseocharitaceae (1/8, Andes), Ixonanthaceae (8/48, tropical), Kirkiaceae (1/8, Africa), Koeberliniaceae (1/1, southern United States, Mexico), Lacistemataceae (2/27, tropical America), Lepidobotryaceae (1/1, tropical Africa), Lepuropetalaceae (1/1, America), Lophiraceae (1/2, tropical Africa), Octoknemaceae (1/6, Africa), Oncothecaceae (1/1, New Caledonia), Paracryphiaceae (1/2, New Caledonia),

Pelliceraceae (1/1, tropical America), Pentadiplandraceae (1/2, Africa), Pentaphyllaceae (1/2, southeastern Asia), Phellinaceae (1/10, New Caledonia), Phyllonomaceae (1/8, tropical America), Plocospermataceae (1/3, Mexico, Central America), Podoaceae (2/3, southeastern Asia), Posidoniaceae (1/2, Mediterranean, Australia), Pterostemonaceae (1/2, Mexico), Roridulaceae (1/2, South Africa), Sargentodoxaceae (1/1, China), Schoepfiaceae (1/35, tropical), Strasburgeriaceae (1/1, New Caledonia), Surianaceae (1/1, tropical coasts), Tetracarpaeaceae (1/1, Tasmania), Tetrameristaceae (1/3, western Malaysia), Toricelliaceae (1/3, Himalayas, China), Trapellaceae (1/2, eastern Asia), Tribelaceae (1/1, temperate South America), and Vivianiaceae (1/30, South America).

It is hoped that the publication of these lists may help to promote the acquisition of cytological information about these families, as well as of such interesting additional groups as *Ctenolophon*, *Disanthus*, and *Piptocalyx*. Extreme care must be taken, however, to insure the accuracy of a few counts in a group made by themselves, as erroneous reports of chromosome number and chromosome morphology for an unknown group are much worse than no information at all.

In the course of preparing this summary statement, a number of families were reviewed for which the existing results indicated very interesting cytological patterns that would amply repay additional investigation. These families include: Acanthaceae, Bignoniaceae, Capparaceae, Combretaceae, Cyclanthaceae, Dilleniaceae, Gentianaceae, Malpighiaceae, Melastomataceae, Nyctaginaceae, Polygalaceae, Santalaceae, Sapindaceae, Sapotaceae, Sterculiaceae, and Verbenaceae. In general, it can be said that the plants of tropical America are very badly in need of cytological study. The extensive reports of S. and G. Mangenot from tropical Africa have shed much light on the plants of that continent, and have in fact included the only cytological reports of Rapateaceae and Humiriaceae, medium-sized and very interesting tropical American families each represented in Africa by a single species. In a similar way, the studies of J. B. Hair in New Zealand and of P. N. Mehra and his associates in the Himalayan region have been outstanding contributions. Other areas of great interest for additional work on chromosome numbers include South Africa, Madagascar, New Caledonia, Australia, and southern Asia.

REVIEW OF THE CHROMOSOME NUMBERS OF ANGIOSPERMS

The following notes are based upon the sources mentioned above, and are arranged according to the system of Cronquist (1968). A persistent difficulty concerns the monophyletic nature of the group in question, whether it be an order, a family, a superorder, or a subclass. If it has been put together of discordant elements, the cytological deductions may be invalid. Nevertheless, it has appeared worthwhile to offer hypotheses, when possible, concerning the original basic chromosome numbers of various groups, and the role that chromosome information can play in evaluating their relationships.

TABLE 1. Basic chromosome numbers in Magnoliales.

1. Austrobaileyaceae	22 ^a	15. Monimiaceae,	
2. Lactoridaceae	20 (or 21?)	s. str.	19 (22, ca. 40, 43), 39
3. Magnoliaceae	19	15a. Hortoniaceae	
4. Winteraceae	13, 43	(Smith, 1972)	19 (Goldblatt, 1974)
5. Degeneriaceae	12	15b. Atherospermata-	
6. Himantandraceae	12	ceae	22 (21?)
7. Annonaceae	7 (Walker, 1972)	15c. Siparunaceae	22
8. Myristicaceae	19, 21, 25	16. Gomortegaceae ^c	21 (Goldblatt, unpubl.)
9. Canellaceae	14 ^b , 13	17. Calycanthaceae	11
10. Illiciaceae	14, 13	17a. Idiospermaceae	11 (Blake, 1972)
11. Schisandraceae	14, 13	18. Lauraceae	12
12. Eupomatiaceae	10	19. Hernandiaceae	20
13. Amborellaceae	13	19a. Gyrocarpaceae	15
14. Trimeniaceae	8 (Goldblatt, 1974)		

^a Peter Goldblatt (1974) has reexamined mitosis in the cuttings from the plant on which Rüdénberg's (1967) report of $2n = 44$ was based. He found that the chromosomes were large, clearly differentiated, and unequivocally $2n = 44$ as reported. We suggest that the "pair of quite small submedian chromosomes" mentioned by Ehrendorfer et al. (1968: 342) may have been satellites, noted by Rüdénberg (1967).

^b Goldblatt (1976a) has determined $2n = 28$ in *Canella alba* Murr. cultivated at the Missouri Botanical Garden.

^c Plants grown in the University of California Botanical Garden, Berkeley, and previously reported as *Gomortega* (Raven et al., 1971), have been redetermined as *Beilschmeidia berteriana* (Gay) Kosterm., which therefore has $n = 12$ and $2n = 24$.

CLASS MAGNOLIOPSIDA (DICOTYLEDONEAE)

I. SUBCLASS MAGNOLIIDAE

I-1. *Magnoliales*.—The basic chromosome numbers in this order are summarized in Table 1. It now appears clear that $x = 7$ is the original basic chromosome number for this order and for the angiosperms (Raven & Kyhos, 1965; Stebbins, 1966; Ehrendorfer et al., 1968; Raven et al., 1971; Walker, 1972). As there is no evidence to support the present or past existence of plants with $n = 6$ or $n = 5$, it seems preferable to explain most of the tetraploid ($x = 12, 13$) numbers of these ancient families by aneuploid reduction from $n = 14$. Whether $n = 10$ in *Eupomatia* and $n = 11$ in *Idiospermum* and Calycanthaceae can be explained in the same way or by aneuploid increase from $n = 7$, as seems to have occurred in Annonaceae (Walker, 1972), remains to be seen. By an extension of this reasoning, Atherospermataceae, Austrobaileyaceae, Gomortegaceae, Hernandiaceae, Lactoridaceae, Magnoliaceae, Monimiaceae, Myristicaceae, and Siparunaceae are paleohexaploid; of these, Atherospermataceae, Siparunaceae, and Gomortegaceae could conceivably have had a common ancestor, whereas all of the other families seem to have been derived independently. The most frequent base number in Winteraceae, $n = 43$, which occurs in all genera except *Tasmannia* ($x = 13$), appears to be of paleododecaploid origin. Cytology provides no evidence for or against subdividing Magnoliales, as Thorne (1968) and Takhtajan (1969) have done.

I-2. *Piperales*.—Chloranthaceae consist of five genera; no chromosome counts are available for the monotypic *Ascarinopsis* of Madagascar. In *Hedyosmum*, $n = 8$ (two species). *Sarcandra* and *Chloranthus* have $x = 15$ (older counts of $2n = 28$ in *Chloranthus* should be confirmed), *Ascarina* (one count), $n = 14$. With the available information, the original basic chromosome number of the family

could be either $x = 7$ or $x = 8$. Saururaceae consist of four genera, with $x = 11$ in *Anemopsis* and *Saururus* and probably $x = 12$ in *Hottuynia* (several high and irregular numbers; apomixis). Piperaceae consist of four genera, including the vast genera *Piper* and *Peperomia*, which have been poorly sampled chromosomally. For *Peperomia*, $x = 11$ (Smith, 1966); the presence of other basic chromosome numbers should be reconfirmed. In *Piper* and *Pothomorphe*, no conclusion regarding basic chromosome number is possible at present, but $x = 12$, 13, and 14 are known; much more work will be necessary before the cytological situation in this genus is clarified. Cytological evidence supports the notion of a close relationship between Saururaceae and Piperaceae, but provides no indication of a relationship between Chloranthaceae and Piperaceae (Swamy, 1953; Smith, 1972). Chloranthaceae might better be placed in the Magnoliales as suggested by Thorne (1968) and Takhtajan (1969, Laurales), leaving the Piperales as a more homogeneous satellite order. This would appear to be supported by the conclusions of Hickey & Wolfe (this symposium).

I-3. *Aristolochiales*.—Aristolochiaceae consist of 7–10 genera, of which chromosome counts are available for three. In *Aristolochia*, there are many diploid species with $n = 7$, and some aneuploid (to $n = 4$) and polyploid derivatives. In *Asarum*, $x = 13$ (in *Asarum* and *Hexastylis*) and 12 (in *Heterotropa*). In the Indo-Malaysian shrubby *Apama*, $n = 13$ is the only available chromosome count. It is reasonable to assume that the basic number for the family and order is $x = 7$, with aneuploid reduction at either the diploid or tetraploid level to produce $x = 13$. Aristolochiaceae have often been considered directly related to Annonaceae, and both have $x = 7$.

I-4. *Nymphaeales*.—Nymphaeaceae consist of *Nymphaea*, $x = 14$; *Nuphar*, $x = 17$; *Euryale*, $n = 29$; and *Victoria*, perhaps $x = 12$. The cytological relationships confirm the morphological and anatomical evidence of a number of very distinct, loosely related genera. *Barclaya*, sometimes segregated as a distinct family (Takhtajan, 1969), has $n = 18$ and possibly $n = 17$. In the group often recognized as Cabombaceae (Takhtajan, 1969; Thorne in Becker, 1973), *Cabomba*, based on several rather old counts, has $n = 12$ and $n = 52$ in the same species and *Brasenia* has $n = 40$. In Nelumbonaceae, the only genus, *Nelumbo*, has $n = 8$, a very distinctive chromosome number even within this heterogeneous group. Taken at face value, this tends to support Takhtajan's (1969) segregation of this family as a distinct order (see also Smith, 1972). Finally, in Ceratophyllaceae, the basic chromosome number of the only genus, *Ceratophyllum*, might be $n = 12$, but the evidence, based on scattered, diverse, and rather old chromosome counts, is insufficient. A detailed chromosomal analysis of Nymphaeales, taking into account chromosome morphology as well as number, appears a promising subject for investigation, even though at least one count is available for all but one of the recognized genera in the order. If *Nelumbo* is excluded, the order may have had a polyploid original basic number.

I-5. *Ranunculales*.—In general, this order is characterized by relatively low chromosome numbers and large chromosomes. In Ranunculaceae, $x = 7$, 8, 9. Podophyllaceae, added to Ranunculaceae by Cronquist (1968), have $x = 6$ in four of the six genera, $n = 7$ in the monotypic, Japanese *Ranzania*. Chromosomally

as well as morphologically they could be regarded as intermediate between Berberidaceae, where they have usually been placed, and Ranunculaceae (Airy Shaw, 1966). In Berberidaceae, $x = 6$ and, in *Berberis* (*Mahonia*), $x = 14$. The Leonticaceae, segregated by Airy Shaw (1966) from Berberidaceae, have $x = 6$ and 8 (7, 9). *Nandina*, considered very distinct in Berberidaceae, is likewise distinct cytologically, with $n = 10$, a unique chromosome number in the order. This would in itself tend to support Takhtajan's (1969) treatment of Nandinaceae as a separate family. The only species of *Circaeaster* (Circaeasteraceae) has $n = 15$. The subfamily Hydrastoideae of Ranunculaceae is very distinct cytologically, with $n = 10$ in *Glaucidium*, $n = 13$ in *Hydrastis*, and this seems to be in accordance with its segregation as a distinct family or families by Airy Shaw (1966) and Takhtajan (1969).

Lardizabalaceae, with $x = 16$, 15, and 14 (see also Ratter & Milne, 1973), and Menispermaceae, with $x = 13$ and 12, have large chromosomes also and chromosome numbers that are clearly secondarily derived within this order. Sabiaceae are also included by Cronquist (1968) here, and *Meliosma*, with $x = 8$, is compatible with the other families of the order on cytological grounds. The segregation of Meliosmaceae from Sabiaceae as a distinct and possibly not closely related family by Airy Shaw (1966) receives support from the only known chromosome number in *Sabia*, $n = 12$. Both Sabiaceae and Meliosmaceae would fit equally well on cytological grounds in Sapindales (Takhtajan, 1969) or Rutales (Thorne, 1968). On chromosomal grounds, Coriariaceae, with $x = 20$ and small chromosomes fit very poorly in this order, as do Corynocarpaceae, with $n = 22$. Coriariaceae appear to fit better in Rosales (Thorne, 1968) or Rutales (Takhtajan, 1969) on the basis of cytology, whereas Corynocarpaceae fit better in Celastrales (Takhtajan, 1969) or Rosales (Thorne, 1968). On the other hand, Papaveraceae, included in the order by Thorne (1968), appear to fit well in the Papaverales (see order I-6).

I-6. *Papaverales*.—Of the three subfamilies of Fumariaceae (Ernst, 1962), $x = 8$ in the unigeneric Hypecoideae and (with various aneuploid derivatives) in the Fumarioideae also. In the monotypic Japanese (and probably relictual) Pteridophylloideae, $n = 9$. In the Papaveraceae, $x = 7$ is common, with $x = 6$ a frequent aneuploid derivative; but among the more primitive, perennial members of the Chelidonioideae (Ernst, 1962), $x = 10$ in *Stylophorum*, *Bocconia*, and *Macleaya* and $x = 9$ in the closely related *Sanguinaria* and *Eomecon*. What is probably a relatively unspecialized member of Papaveroideae, *Romneya*, has $n = 19$. Considering that Fumariaceae are on morphological grounds clearly derived from Papavaraceae, and taking into account the distribution of these chromosome numbers, $n = 10$ appears to be the original basic chromosome number for the order, and for Papaveraceae, and $n = 9$ the original basic chromosome number for Fumariaceae.

II. SUBCLASS HAMAMELIDIDAE

II-1. *Trochodendrales*.—The only species of Tetracentraceae has $n = 24$ (possibly 23, Ratter & Milne, 1973; Ratter, personal communication) and not $n = 19$ as reported earlier by Whitaker (1933). The only species of Trochodendra-

ceae, on the other hand, has $n = 20$ (Ratter & Milne, 1973) and not $n = 19$ as reported by Whitaker (1933). As pointed out by Ratter & Milne (1973), cytological evidence could be used to support Hutchinson's (1959) association of *Euptelea* ($n = 14$) with *Trochodendron*, if the genera are respectively tetraploid and hexaploid on $x = 7$.

II-2. *Hamamelidales*.—Among the smaller families of this order, Cercidiphyllaceae have $n = 19$, Eupteleaceae $n = 14$, Platanaceae $n = 21$ (with a series of other dubious reports), and Myrothamnaceae and Didymelaceae are unknown. In the central family, Hamamelidaceae, both the very distinct *Liquidambar* and the genus *Altingia*, sometimes segregated with it as a separate family, Altingiaceae, have $n = 16$ (Santamour, 1972; P. Goldblatt, unpublished). The only count available for the Exbucklandioideae, $n = 32$ in *Exbucklandia populnea* (R. Br. ex Griff.) R. W. Brown [as *Symingtonia populnea* (R. Br. ex Griff.) van Steenis; Mehra & Khosla, 1972], is in agreement with a base chromosome number of $x = 16$. In contrast, the Hamamelidoideae, based on abundant determinations of chromosome number, uniformly have $x = 12$ (8 genera), *Rhodoleia teysmannii* Miq., the only species of Rhodoleioideae for which chromosomal information is available, likewise has $n = 12$ (Goldblatt, unpublished). Counts for the monotypic Disanthoideae would be welcome. The chromosomal evidence indicates a fundamental gap between the Hamamelidoideae and Rhodoleioideae on the one hand and the Liquidambaroideae (with *Altingia*) and Exbucklandioideae on the other.

II-3. *Eucommiales*.—The only species has $n = 17$.

II-4. *Urticales*.—Ulmaceae may have had original basic chromosome numbers of $x = 14$ and $x = 10$, the former in *Ulmus*, *Zelkova*, and probably *Holoptelea* and the latter in *Celtis* (other reports need to be confirmed), *Chaetachme*, and *Trema*. How these two chromosome numbers relate is unknown, and more records for the family would be highly desirable. Moraceae probably also had $x = 14$, with $x = 13$ a frequent derivative. Aneuploidy is common in *Dorstenia*. Cannabaceae have $n = 10$ in both genera, although lower numbers have also been reported in *Humulus*. On cytological grounds, they do not appear closely related to Moraceae, and may represent the end product of another evolutionary line; their segregation at a family level appears warranted. In Urticaceae, $x = 14$, 13 and 12 are all well represented, with $x = 11$, 10, 8, and 7 found in some genera. *Parietaria* has $n = 7$, 8, 10, and 13, and the only species of *Pellonia* counted to date has $n = 8$; both genera would doubtless be rewarding subjects for further cytological investigation. For the order Urticales and the families Ulmaceae, Moraceae, and Urticaceae, an original basic chromosome number of $n = 14$, itself tetraploid, seems clearly to be indicated, with subsequent aneuploid reduction in Urticaceae and in the evolution of Cannabaceae. The presence of both $x = 10$ and $x = 14$ in Ulmaceae is the least understood cytological feature of the order. The monotypic Barbeyaceae are unknown cytologically, but recognized as a distinct order by Takhtajan (1969).

II-5. *Leitneriales*.—The single species has $n = 16$, as does Juglandales.

II-6. *Juglandales*.—Juglandaceae have $x = 16$. The West Indian Picrodendraceae, placed by Thorne (1968) in Euphorbiaceae and by Airy Shaw (1966) near

that family, are unknown cytologically, as are Rhoipteleaceae, consisting of a single species of tropical Asia with a wood structure similar to that of Aceraceae.

II-7. *Myricales*.—The only family, Myricaceae, has $x = 16$, as does Juglandales. Perhaps the preceding three orders are better placed in Rutiflorae where they would be morphologically and anatomically better matched (Thorne, 1968). Cytologically the matter is not clear.

II-8. *Fagales*.—Fagaceae have $x = 12$ (scattered records of $x = 11$ and $x = 10$ require confirmation), except for *Nothofagus*, with $n = 13$. The ditypic and presumably relictual *Trigonobalanus* has $n = 22$ (Soepadmo, 1972). Recently, $2n = 28$, together with $2n = 26, 30$, and 32 has been reported for *Quercus castaneifolia* C. A. Meyer (Tutajuk & Turchaninova, 1970), but these numbers were said to occur together in the same tissues, as did $2n = 24$, probably the actual chromosome number in this species as in other oaks. Betulaceae have $x = 14$ in *Alnus*, *Betula*, and *Corylus*, and $x = 8$ in *Carpinus*, *Ostrya*, and *Ostryopsis* (Carpinaceae), which are therefore a very distinct group within the order cytologically. The original basic chromosome number for the order may have been $n = 7$, with early polyploidy. Balanopaceae, very doubtfully related to Fagales (R. F. Thorne, personal communication), are unknown cytologically.

II-9. *Casuarinales*.—The original basic chromosome number in *Casuarina*, the only genus, is very probably $x = 9$, with a considerable number of aneuploid changes in the course of evolution (Barlow, 1959; Smith-White, 1959). In subg. *Gymnostoma*, the more primitive of the two subgenera, $n = 8$ in the only species counted. On cytological grounds, Casuarinales fit reasonably within Cronquist's (1968) subclass Hamamelididae; most morphological similarities may be attributable to convergent evolution for anemophily.

III. SUBCLASS CARYOPHYLLIDAE

III-1. *Caryophyllales*.—Phytolaccaceae, although poorly sampled, have an original basic chromosome number of $x = 9$, and all taxa examined, including *Petiveria*, have some multiple of that number. Gyrostemonaceae, regarded as a distinct family by Thorne (1968) and Takhtajan (1969), have $n = 14-15$ (P. Goldblatt, unpublished) and are certainly not related to the other families of Caryophyllidae. No information is available for the recently recognized Halophytaceae and Hectorellaceae. Cactaceae have $x = 11$, with relatively little aneuploidy or polyploidy. Aizoaceae (and Tetragoniaceae; Takhtajan, 1969) have $x = 9$, with a few aneuploid changes, especially to $x = 8$. Molluginaceae also have $x = 9$. Basellaceae probably have $x = 12$, with $x = 11$ in *Basella rubra* L. Chenopodiaceae have $x = 9$, with very little aneuploidy but frequent polyploidy. Amaranthaceae and Portulacaceae have some genera with $x = 9$, but such abundant aneuploidy that it would not be possible without detailed study of the respective families to ascertain the original basic chromosome numbers. Nyctaginaceae, although they are cytologically difficult, display such an array of chromosome numbers among the relatively few taxa that have been counted that it would clearly be of great interest to know more. The two species of Didiereaceae that have been examined cytologically had $2n = \text{ca. } 150$ and $2n = \text{ca. } 190-200$, respectively.

In Caryophyllaceae, subfamily Paronychioideae have $x = 9, 10$ and 8 ; subfamily Alsinoideae, $x = 10, 11, 12, 13$, with $x = 9$ in *Cerastium* and $x = 14$ in *Myosoton*; and subfamily Silenoideae, $x = 12$, with $x = 10$ in *Vaccaria* and *Drypis*. Some species of *Paronychia* and the monotypic *Chaetonychia* have $n = 7$, evidently as a result of descending aneuploidy.

Considering that Phytolaccaceae are, in many respects, the most generalized family of the order, and considering the distribution of chromosome numbers among the other families, it appears likely that $x = 9$ is the original basic chromosome number for Caryophyllales.

III-2. *Batales*.—*Batis*, the only genus, has $n = 9$, a number compatible with Caryophyllales.

III-3. *Polygonales*.—Frequent basic chromosome numbers in the Polygonaceae, the only family, are $x = 10, 11$, and 12 , with $x = 7, 8$, and 9 represented in the tribe Rumiceae, $x = 9$ in *Calligonum*, and $x = 9$ in two species of *Eriogonum*. Chromosome numbers below $n = 10$ in Polygonaceae seem clearly to have been derived by aneuploid reduction.

III-4. *Plumbaginales*.—In Plumbaginaceae, the only family, $x = 7$ in Plumbagineae without much doubt, with $x = 8$ possibly the original basic chromosome number in Staticeae (H. G. Baker, personal communication), judging by its occurrence in the relatively unspecialized *Gomiolimon* and *Acantholimon*, as well as (together with $n = 9, 7$, and 6) in *Limonium*. Since Plumbagineae are manifestly not as specialized as Staticeae, $x = 7$ may cautiously be advanced as the original basic chromosome number for the family, as suggested by H. G. Baker (personal communication). Cytological evidence does not therefore support the placement of this family in Caryophyllidae.

IV. SUBCLASS DILLENIIDAE

IV-1. *Dilleniales*.—Very few chromosome counts are available for the phylogenetically critical Dilleniaceae. It may be that $x = 8$ in *Dillenia* and *Hibbertia*; the only count available for *Tetracera* is $n = 12$, and the only one for *Wormia* is $n = 13$. For *Curatella americana* L., $n = 13$ and ca. 12 have been reported. It would be of very great interest to obtain more information. Paeoniaceae, $x = 5$, and Crossomataceae, $x = 12$, are very distinct from one another cytologically (Raven & Cave, 1963).

IV-2. *Theales*.—For Ochnaceae, $x = 12$ in two genera, 14 in two others (*Ouratea* has predominantly $x = 14$; one species has $n = 13$, Bawa, 1973), and $x = 19$ in *Sauvagesia*. The latter number, coupled with reports of $2n = 35$ in *Ochna serrulata* Walp., strongly suggests an original basic chromosome number for the family of $x = 7$, with aneuploid decrease from $n = 14$ to $n = 12$. Strasburgeriaceae, recognized as a distinct family by Thorne (1968) and Takhtajan (1969), are unknown cytologically, as are Marcgraviaceae, Caryocaraceae, Quiinaceae, Medusagynaceae, Sarcolaenaceae and Sphaerosepalaceae (Rhopalocarpaceae), the latter placed by Thorne (1968) in the order Malvales; Dipterocarpaceae have $x = 7, 6, 11$, and 10 . In Theaceae, $x = 21$ in the related genera *Adinandra* and *Eurya*, with $n = 22$ and $n = 23$ in other species of *Eurya*; x apparently $= 10$ in *Ternstroemia*; $x = 15$ in several genera; and $x = 18$ in the monotypic *Franklinia*,

which is closely related to *Gordonia* and *Stewartia* with $x = 15$, a number also found in the Asian *Schima*. It might be that $x = 7$ is the original basic chromosome number for the family, with increasing aneuploidy and subsequent polyploidy; but many more chromosome counts will be necessary before this can be determined with any degree of certainty. The monogeneric Stachyuraceae have $n = 12$. In Actinidiaceae, *Saurauia* has $n = 30$ and *Actinidia* a series of high chromosome numbers of which $n = 29$ is the lowest reported. Clusiaceae (Guttiferae) appear to have $x = 7, 8, 10$ and perhaps 9 as important basic numbers (Robson & Adams, 1968). For *Hypericum*, Robson and Adams suggest $n = 12$ as the original basic chromosome number, with descending aneuploidy to $n = 7$. More chromosomal information is required for a clear understanding of evolution in this family. For Elatinaceae, scattered counts indicate $x = 9, 10$, and 12.

No definite conclusion can be drawn as to a possible original basic chromosome number for Theales, but $x = 7$ is an important number, with ascending aneuploidy evidently frequent.

IV-3. *Malvales*.—For Elaeocarpaceae, $n = 14$ in *Aristoelia* and *Muntingia*. There is one count each of $n = 12$ and $n = 15$ in *Elaeocarpus*, and *Sloanea* has $n = 13$. The two chromosome counts available for Scyttopetalaceae, each from a different genus, are $n = 11$ and $n = 18$. In Tiliaceae, $x = 9$ and 8 are important basic chromosome numbers, with $x = 10$ in Brownlowioideae and $x = 7$ in *Corchorus*. In the cytologically very interesting Sterculiaceae, $x = 10$ is a recurrent basic chromosome number in several groups; numbers are reduced to $n = 6$ in two genera of Hermannieae; and basic numbers of $x = 18, 20$ and 21 occur in Sterculieae. The original basic chromosome number might be $x = 10$. Bombacaceae have high chromosome numbers and are difficult cytologically: $n = 36$ is most frequent with $n = 72$ (Baker & Baker, 1968), but other numbers such as $n = 43, 44, 45, 46$, and 48 (e.g., Bawa, 1973) also occur. Counts of $n = 14$ and 28 have been reported for *Durio zibethinus* L., but are badly in need of confirmation. Malvaceae, well sampled but very complex cytologically, seem to have $x = 7$ in the tribes Malveae (Bates & Blanchard, 1970; D. M. Bates, personal communication) and Ureneae, $x = 13$ in Gossypieae, and a variety of mostly higher numbers in Hibisceae. For Malvales as a whole, $x = 7$ is an important basic chromosome number, but $x = 10$ appears likely at present for Sterculiaceae and Tiliaceae, perhaps as an ancient reduction from $n = 14$. The same might be true for a hypothetical $x = 12$ (H. G. Baker, personal communication) in Bombacaceae. In Malvaceae, $x = 7$ is probably the original basic chromosome number, as suggested by Krapovickas (1972).

IV-4. *Lecythidales*.—For Lecythidaceae, *sensu stricto*, a tropical American group, one count of $n = 17$ has been obtained for *Bertholletia*, one of $n = 18$ for *Couroupita*; there are some 15 genera. For the Old World tropical family Barringtoniaceae, not recognized by Cronquist (1968), $x = 13$ in three of five genera. *Napoleona*, one of the two genera of Napoleonaceae, has two species counted with $n = 16$. No counts are available for the monotypic Brazilian *Asteranthos*, also segregated by some students as a distinct family. Cytological evidence is not in agreement with Takhtajan's (1969) placing Lecythidaceae

sensu lato, in Myrtales; the known pattern is more compatible with a position in Dilleniales (Theales; Thorne, 1968), or near that order (Cronquist, 1968).

IV-5. *Sarraceniales*.—In Sarraceniaceae, $n = 13$ in all species of *Sarracenia* that have been examined cytologically, $n = 15$ in the monotypic *Darlingtonia*, and $n = 21$ in the monotypic *Heliamphora*. *Nepenthes*, only genus of Nepenthaceae, had $n = 39$ in the two species that have been reported. In Droseraceae, *Dionaea* has $n = 16$; *Drosophyllum* $n = 6$; *Allovandra* $n = 19$ ($24?$); and *Drosera* $x = 10$ in most species, but $n = 13, 14, 16, 17$, and 23 have also been reported, the last two counts both in *D. binata* Labill. In the system of Thorne (1968) these families are widely separated, but Cronquist (1968) does not argue for a close relationship either; cytology certainly provides no indication of a close relationship between them.

IV-6. *Violales*.—In Flacourtiaceae, with some 93 genera and 1000 species, representatives of 12 genera and 19 species have been reported, with basic chromosome numbers of $x = 12$ and 11 most frequent. The only count for *Oncoba* was $n = 10$. Two species of *Flacourtia* had $n = 11$, one, $n = 9$. The bigeneric Lacistemaceae have not been examined cytologically, nor have Achariaceae, Ancistrocladaceae, Hoplestigmataceae, or Peridiscaceae. The only reported count for Dioncophyllaceae was $n = 18$. The monotypic Scyphostegiaceae have $n = 9$ (Ding Hou, 1972). Violaceae have *Rinorea* with $x = 12$, *Decorsella* with $n = 10$, *Hymenanthera* and *Melicytus* with $x = 16$ (based on $x = 8?$), *Hybanthus* with $x = 6$ and 4 (Bennett, 1972); and *Viola* perhaps with $x = 12$ but aneuploidy down to $n = 5$ and up to $n = 13$ (or 17). Turneraceae, on the basis of few counts, have $x = 5$ in *Turnera* (R. Ornduff, personal communication) and $n = 7$ in *Piriqueta*. Passifloraceae have $x = 12$ in two genera, $n = 11$ in two others, and $x = 9$ in *Passiflora* (two species with $n = 6$ doubtlessly derived). Malesherbiaceae, with a single genus, have $x = 7$. Bixaceae have $n = 7$ and $n = 8$ both reported in *Bixa*, which ought to be examined further, and $n = 6$ in *Cochlospermum*, the large chromosomes and low numbers of these two genera being in accordance with Cronquist's merging of Cochlospermaceae with Bixaceae. In Cistaceae, $x = 12$ in *Tuberaria*, with $n = 7$ in one species; $x = 12, 11, 10$ (commonest number), 9 , and 5 in *Helianthemum*; $x = 9$ in *Cistus* and *Halimum*; and $x = 16$ (probably $x = 8$) in *Fumana*. All species of Tamaricaceae that have been counted have $n = 12$. On the basis of five species of *Frankenia* counted, Frankeniaceae seem to have $x = 5$. Fouquieriaceae have $x = 12$, thus agreeing with Tamaricaceae, but also with Solanales where they are placed by Thorne (1968). Caricaceae have $x = 9$ in *Carica*, the only genus for which counts are available. Loasaceae may have $x = 7$ (H. J. Thompson, personal communication), with $x = 14$ in *Loasa* and *Mentzelia*, $n = 13$ in *Cevallia*, $n = 21$ in all species of *Eucnide*, $n = 12$ in *Blumenbachia*, $n = 8$ and 7 in *Caiophora*, and $n = 37$ in *Gronovia*. Cytologically the family would fit equally well in Polemoniales, where it is placed by Takhtajan (1969). In *Begonia*, the only genus of the family that has been examined cytologically, all gametic chromosome numbers from $n = 8$ to 18 , as well as many higher numbers, have been reported. The number $n = 14$ is most frequent, and R. A. H. Legro (personal communication) has suggested a hypothetical original basic chromosome number for the family of $x = 7$. Datisceae have *Datisca* with $n = 11$ and

Tetrameles with $n = \text{ca. } 23$. Cucurbitaceae (Jeffrey, 1962) commonly have basic chromosome numbers of $x = 12$ and 11 , less commonly $x = 13, 14, 10, 9$, and 8 . Cytologically, they are very similar to the closely related Passifloraceae. *Mormordica*, of the tribe Joliffieae, has both $n = 14$ and $n = 11$; in Cucurbitaceae, *Luffa* has $n = 13$ and $n = 11$; and in Melothrieae, the monotypic South American *Cucurbitella* has $n = 13$. *Seyrigia* (Madagascar), the only genus of the mostly tropical American Anguriinae for which cytological information is available, has $n = 13$ also. Cyclanthaceae have $x = 8$. Considering the distribution of these counts, $x = 13$ or even $x = 14$ may be suggested as the original basic chromosome number of the family. For the order, $x = 7$, with early tetraploidy and aneuploid reduction preceding the origin of several families, seems likely at present.

IV-7. *Salicales*.—All three genera have $x = 19$.

IV-8. *Capparales*.—For Capparaceae, which are interesting cytologically but have been relatively poorly sampled, $x = 10$ or 11 might be a likely original basic chromosome number, judging from its representation in subfamilies Capparoideae and Cleomoideae. If that proves to be the case, there has been descending aneuploidy in both lines and then the formation of the secondary polyploid number $x = 17$ in *Cleomella* and some species of *Cleome*. In Brassicaceae, *Stanleya*, *Pringlea*, and *Ornithocarpa* (Rollins, 1969), three of the least specialized genera, have $x = 12$, as do *Draba* (with descending aneuploidy to $x = 8$; G. A. Mulligan, personal communication), *Selenia*, *Orychophragmus*, *Brassicella*, *Kremeria*, *Aethionema*, *Rhynchosinapis*, and some species of *Thlaspi* (also $x = 7$), *Sinapis* (also $x = 9, 7$), *Lobularia* (also $x = 11$), *Iberis* (also $x = 11, 10, 9, 7$), *Ionopsidium* (also $x = 11, 8$), and *Brassica* (also $x = 11, 10, 9, 8$). Genera in which $x = 11$ are *Xerodraba*, *Parolinia*, *Menonvillea*, *Morettia*, *Notoceras*, and *Eruca*, as well as some species of *Leavenworthia*, *Nerisyrenia*, *Diplotaxis*, *Smelowskia* ($n = 6$ also reported), *Ionopsidium*, *Iberis*, and *Heliophila*. Although the base number $x = 7$ is frequent in this family, $x = 6$ is very scattered and occurs either in obviously specialized genera or in descending aneuploid species within genera. The lowest chromosome numbers in the family occur in the Australian *Stenopetalum* and the American *Physaria*, $x = 4$ (also $x = 5$ in both, and $x = 6$ in *Stenopetalum*). At this time, $x = 12$ appears a reasonable choice for the original basic chromosome number of Brassicaceae, even though $x = 13$ and 14 are found in such primitive genera as *Streptanthus*, *Thelypodium*, and *Caulanthus*, and $x = 14(7)$ might ultimately prove to be correct. In Resedaceae, $x = 10$ occurs in three of the four genera for which chromosome information is available, with $x = 6$ also present in *Reseda*. For *Oligomeris*, counts of $n = 14$ and $n = 24$ have been reported for the only species examined. The three species of *Moringa*, only genus of Moringaceae, which have been examined cytologically all had $n = 14$. For the original basic chromosome number of the order, $x = 12, 11$, or 10 appear the most likely candidates on the basis of information currently available. No counts are available for Tovariaceae.

IV-9. *Ericales*.—Cyrillaceae have $x = 10$, Clethraceae $x = 8$. In Ericaceae, $x = 12$, found in all four subfamilies, may be the original basic chromosome number, with $x = 13$ and 11 frequent aneuploid derivatives, and $x = 7, 8$, and 16

found in one genus each. The cytologically very diverse Epacridaceae seem to have $x = 6$ (Smith-White, 1959), which suggests that the closely related Ericaceae may have had a tetraploid origin. Empetraceae have $x = 13$. In Pyrolaceae two genera probably have $x = 13$, one $n = 19$, and *Pyrola* $x = 23$ ($n = 12$ also reported, possibly reliably). Monotropaceae have $x = 8, 13, 14$, and possibly $x = 11$. In the evolution of Ericales, $x = 6$ was probably the original basic chromosome number, with $x = 12$ being present in the common ancestor of Ericaceae, Pyrolaceae, and Monotropaceae, but $x = 13$ possibly in the common ancestor of the last two families, as in the ancestor of Empetraceae. On cytological grounds, Cyrillaceae and Clethraceae seem to fit poorly in this order, and have chromosome numbers that accord better with those in Theales, where they are placed by Thorne (1968).

IV-10. *Diapensiales*.—The only family, Diapensiaceae, has $x = 6$, as postulated for Ericales. This seems to support its placement here rather than in Rosales as suggested by Thorne (1968).

IV-11. *Ebenales*.—Sapotaceae have $x = 12$ in 10 of the genera for which counts are available, $x = 13$ in five, $x = 11$ in two, and $x = 10$ in one, and $n = 13$ and $n = 22$ are both reported for *Sideroxylon*. Ebenaceae, certainly closely related to Sapotaceae, have $n = 15$ (F. White, personal communication), with $n = 12$ reported once (Gadella, 1972). Styracaceae have $n = 8$ in *Styrax*, $n = 12$ in *Pterostyrax* and *Halesia*. For Symplocaceae, $x = 11$ has been reported for seven Asian species of *Symplocos*, $n = 12$ for one from Puerto Rico. For Ebenales, only a very tentative suggestion of $x = 12$ as the original basic chromosome number can be made. No counts are available for Lissocarpaceae.

IV-12. *Primulales*.—Theophrastaceae have $x = 18$ in *Jacquinia* and *Claviija* ($n = 20$ also reported), and $n = 13$ in one report of *Deherainia*. Myrsinaceae have $x = 12$ and $x = 10$, with several genera, including *Aegiceras* ($x = 23$), polyploid. Judging from its distribution and relationship with $x = 23$, $x = 12$ is almost certainly the original basic chromosome number. Primulaceae might have $x = 12$, with $x = 12, 11, 10, 8, 15$, and 28 in the tribe Lysimachieae; $x = 12, 11, 10, 14, 15$, and 17 in Cyclamineae; $x = 12, 11, 10$, and (in *Primula*) 9 and 8 , as well as secondarily polyploid numbers in Primuleae; and $x = 12, 13$, and 18 in *Samolus*, only genus of Samoleae. The monotypic *Coris*, sometimes segregated as a distinct family, has $n = 9$, which is certainly distinctive in Primulaceae. It is possible that $x = 12$ for Primulales.

V. SUBCLASS ROSIDAE

V-1. *Rosales*.—One species of Eucryphiaceae has $n = 15$ (P. Goldblatt, unpublished). Cunoniaceae have $n = 12$ in *Pancheria*, $n = 16$ in four genera, including *Cunonia*, and $n = 15$ in its relative, *Weinmannia*. More counts are highly desirable. Bauera, sometimes segregated as a distinct family, has $n = 16$. The monotypic Davidsoniaceae have $n = 16$ also (B. G. Briggs, personal communication). No counts are available for Brunellia. Pittosporaceae have $n = 12$ in *Pittosporum* and *Sollya* and $n = 18$ in *Citriobatus*. For Byblidaceae, $n = 7$ and $n = 12$ are reported for the two species of *Byblis*, respectively. For Hydrangeaceae, $x = 13$ is a frequent basic number, with $x = 11, 10, 14, 18, 17$, and 16 also

represented. *Carpentaria*, a monotypic genus of California with $n = 10$, might be related to an early aneuploid reduction. The original basic number for the family might be $x = 7$. For the elements of Cronquist's (1968) very inclusive Grossulariaceae, the following results are available—Brexaceae: *Ixerba*, $n = 25$; *Brexia*, $n = 32$. Escalloniaceae: *Escallonia*, $n = 12$; *Carpodetus*, $n = 15$ (14?). Iteaceae: *Itea*, $n = 11$. Montiniaceae: *Montinia*, $n = 34$ (Goldblatt, 1976a). Grossulariaceae, sensu stricto: *Ribes*, $n = 8$. Polyosmeae, $n = 16$. In Bruniaceae, the unspecialized genus *Audouinia* has $n = 11$; other genera are evidently palaeopolyploid with $x = 22$ in *Staavia*, *Lonchostoma* and *Raspalia*, probably $x = 23$ in *Brunia* and *Nebelia*, while the most advanced genus, *Berzelia*, has $x = 20$ (Goldblatt, 1976b).

Cronquist's Saxifragaceae includes groups segregated as follows—Francoaceae, $x = 13$ (one count). Parnassiaceae, $x = 9$ (8?). Penthoraceae, $x = 8, 9$. Vahliaceae, $x = 6$. Saxifragaceae, sensu stricto, $x = 7$, with aneuploidy in several genera. *Chrysosplenium* does not fit well cytologically with the rest of the Saxifrageae-Leptarrheneae-Astilbeae, as it has $x = 12$ (11? 9?).

Crassulaceae very likely have $x = 9$, with early aneuploid reduction and some increase, together with the formation of secondary basic numbers such as $x = 17$, common in the family. *Sedum* has every gametic chromosome number from $n = 4$ to $n = 12$ inclusive.

Rosaceae have been much studied and discussed cytologically, primarily because it was realized early that the base number of subfamily Pomoideae was $x = 17$, and the group is therefore of paleotetraploid origin (Sax, 1931, 1933). In subfamily Prunoideae, including *Exochorda*, $x = 8$, and in Spiraeoideae $x = 9$. It has been suggested that Pomoideae might be of tetraploid origin from the stocks that eventually led to the evolution of these large groups, but this no longer appears to be likely, as there is evidently no direct relationship between Prunoideae and Pomoideae (W. G. D'Arcy, personal communication). In Rosoideae, $x = 7$ is the common base number, but $x = 9$ occurs in several lines, including the more primitive woody genera of Dryadeae and Kerrieae, and $x = 8$ is the base number in the subtribe Alchemillinae. Isolated groups of special interest within Rosaceae recently counted by Peter Goldblatt (1976c) include *Kageneckia*, $n = 17$ (all 3 species); *Quillaja*, $n = 14$ ($n = 17$ also reported, evidently in error); and *Vauquelinia* (3 species), $n = 15$. *Lyonothamnus*, another morphologically isolated genus, fits chromosomally into Spiraeoideae and with other relatively primitive roses with $n = 27$, which certainly does not suggest a close relationship with *Vauquelinia*. In view of this distribution, it seems possible that the original basic chromosome number of Rosaceae was $x = 9$, but there were certainly several instances of aneuploid reduction and perhaps increase, as well as the early polyploid origin of Pomoideae. Reduction to $x = 7$ in the evolution of Rosoideae must have taken place very early, considering the fact that Sanguisorbeae are common to Africa and South America, with woody, evidently relict genera on each continent; this might even be the original basic chromosome number for the family.

Of the families related to Rosaceae, Neuradaceae have $x = 7$ and Chrysobalanaceae $n = 11$ in three genera with $n = 10$ in *Parinari*. For Fabaceae,

Caesalpinioideae might have $x = 7$, with early polyploidy and reduction from $n = 14$ to $n = 11$. Base numbers of $x = 8$ occur in a few genera scattered through many groups, and seem to have arisen early also; $x = 10$ occurs in *Pterogyne*. Although $x = 8$ has been proposed as the original basic chromosome number of Papilionoideae by Senn (1938), and of Caesalpinioideae by Turner & Fearing (1959), $x = 7$ appears to be another possibility in view of the distribution of polyploid chromosome numbers of apparently relictual genera, especially in Caesalpinioideae (Turner & Fearing, 1959). Mimosoideae evidently have a basic chromosome number of $x = 7$, with the derived numbers $x = 13$ and 14 frequent, and $x = 8$ in several lines, but $n = 8$ apparently no longer represented. For Faboideae, $x = 7$ is common to all tribes except Phaseoleae and Dalbergieae, which have basic chromosome numbers that might in part at least be derived from $n = 14$; but many aneuploid derivatives, if the hypothesis of $x = 7$ as the original basic chromosome number is correct, have been established early in the history of the group.

Summarizing for Rosales, $x = 7$, 8 , and 9 all appear candidates for the original basic chromosome number for the order, with an ultimate derivation from $x = 7$. Connaraceae, usually included with Rosales but allied by Cronquist (1968) with Sapindales, fit very well chromosomally in Rosales, with $n = 14$ in six genera, $n = 13$ in one. On the other hand, chromosomal evidence does not provide additional evidence for the placement of Crossosomataceae (Thorne, 1968) in Rosales any more than in Dilleniales (Cronquist, 1968; Takhtajan, 1969), or of Staphyleaceae here (Thorne, 1968) rather than in Sapindales (Cronquist, 1968; Takhtajan, 1969). No chromosome counts are available for Eucryphiaceae, Davidsoniaceae, Byblidaceae, Columelliaceae, or Alseuosmiaceae.

V-2. *Podostemales*.—Judging from three counts from as many genera, $x = 10$ for the only family of this order. There are 45 genera and 130 species in the group.

V-3. *Haloragales*.—For Haloragaceae and Hippuridaceae, $x = 7$. For Gunneraceae, with only *Gunnera*, $n = 17$, with two reports of $n = 12$ which require confirmation. The chromosomal information available concerning *Gunnera* supports its segregation as a distinct family (Thorne in Becker, 1973). For *Theligonum*, only genus of Theligonaceae, both $n = 10$ and 11 have been reported.

V-4. *Myrtales*.—Sonneratiaceae have $x = 12$ in *Duabanga* and $n = 9$ in one count from *Sonneratia*. Lythraceae probably have $x = 8$, which is also the basic chromosome number in most genera (S. A. Graham, personal communication), with $n = \text{ca. } 10$ in *Lafoensia*, $n = 30$ in *Nesaea*, and $x = 5$ in *Lythrum*. For Penaeaceae, $x = 10$ as far as known at present. Thymelaeaceae very clearly have $x = 9$. Trapaceae consist only of *Trapa*, with $x = 12$. Myrtaceae definitely have $x = 11$ (Smith-White, 1959). Heteropyxidaceae, recognized and placed in Rhamnales by Hutchinson (1959), but submerged in Myrtaceae by most recent authors, has $x = 12$ like Rhamnales but also some Myrtales. *Punica granatum* L., one of the two species of the only genus of Punicaceae, has $n = 8$ with up to 3 B-chromosomes (Mehra & Gill, 1971; P. K. Khosla, personal communication). Onagraceae have $x = 11$, which is the only basic number in the most primitive tribe, Fuchsieae, and in Circaeae, and is found in the least specialized taxa of

Lopezieae and Onagreae also. Other chromosome numbers in the family have been derived by descending aneuploidy. Melastomataceae, with some 240 genera and 3000 species, have been very inadequately sampled, despite the wide range displayed by the approximately 75 counts that have been reported for about 30 genera. For subfamily Memecyloideae, $x = 7$ in *Memecylon* and $n = 12$ in the only species of *Mouriri* examined to date; unfortunately *Axinandra*, phylogenetically critical (Meijer, 1972), has yet to be examined cytologically. For the rest of the family, it can only be said that $x = 14$, 12, and 9 are common basic numbers, with all gametic numbers from $n = 8$ to $n = 19$ represented in one or more genera. For Crypteroniaceae, if circumscribed as proposed by Beusekom-Osinga and Beusekom (1975), *Rhynchochalyx* has $n = 10$ (Goldblatt, 1976a). For Combretaceae, $x = 12$ is the most likely original basic chromosome number, with aneuploid increase in *Quisqualis* and *Combretum*. Reports of $n = 7$ and $n = 13$ in Indian species of *Terminalia*, as by Nanda (1962), have not been reconfirmed (P. K. Khosla, personal communication). One species of *Olinia* has $n = 12$ (Goldblatt, 1976a). For Myrtales as a whole, considering that $x = 12$ in Sonneratiaceae, Trapaceae, Oliniaceae, and Combretaceae, and that this might be the base for Melastomataceae, one might guess that either it or, less plausibly, $x = 11$, definitely the original basic chromosome number in Myrtaceae and Onagraceae, would be the original basic number. No counts are available for Dialypetalanthaceae.

V-5. *Proteales*.—For Proteaceae, $x = 7$ (Johnson & Briggs, 1963). Eleagnaceae, on the other hand, appear to have $x = 14$ in *Elaeagnus* and $x = 12$ in *Hippophaë*, and $x = 11$ (13?) in *Shepherdia*, from which $x = 7$ could be inferred for them also. In *Hippophaë*, $n = 6$ has been reported by Darmer (1947) but doubted by Rousi (1965, 1971); the existence of such a chromosome number should be checked at the original locality, Hiddensee in the Baltic. Chromosomal evidence tends to support Cronquist's (1968) and Takhtajan's (1969) alliance of these two families, but definitely is in conflict with a derivation from Thymelaeaceae or Myrtales, as it is very probably related directly to $x = 7$, the original basic chromosome number of angiosperms.

V-6. *Cornales*.—The monotypic Davidiaceae have $n = 21$ (P. Goldblatt, unpublished). Nyssaceae, Garryaceae, and Alangiaceae have $x = 11$, with $n = 21$ also in the monotypic *Camptotheca* (Nyssaceae; Perdue et al., 1970). Within Cornaceae, the monotypic southern African Curtisiaceae have $n = 13$ (P. Goldblatt, unpublished); Mastixioideae $n = 13$ and 11 (P. Goldblatt, unpublished); and Cornoideae probably $x = 11$, with descending aneuploidy to $n = 9$ in the *Cornus* complex. Among the more distantly related genera assigned to this subfamily, *Aucuba* has $x = 8$, *Griselinia* $n = 18$, and *Helwingia* $x = 19$. The chromosome number of the Himalayan and west Chinese *Toricellia* is unfortunately unknown. The chromosome number of *Corokia*, $n = 9$, provides no evidence for its placement in Cornales or Saxifragales, although the arguments of Eyde (1966) for the latter disposition appear convincing.

For the order Cornales, the existence of $n = 13$ in *Curtisia* and at least one species of *Mastixia* suggests that $n = 13$, or possibly even $n = 14(7)$ might be the original basic chromosome number, with early reduction to $n = 11$. *Aucuba*,

Griselinia, and *Corokia* stand out as sharply chromosomally as they do morphologically. If the hypothesis as to original basic chromosome number for the order presented here is correct, it would be implied that Nyssaceae, Garryaceae, and Alangiaceae are more closely related to Cornoideae than are Curtisioidae and Mastixioidae.

It would be desirable to obtain chromosome counts of *Argophyllum* (Escalloniaceae) and of such genera as *Melanophylla* and *Kaliphora* as part of an investigation of their affinities. Rhizophoraceae have $n = 32$ in Macarisiaceae and $n = 18$ in Rhizophoreae, suggesting base numbers of $x = 8$ and 9, but not supporting a close relationship with either Cornales or Myrtales. They might better be placed with Myrtales (Takhtajan, 1969), as the Cornales are, on the whole, a more homogeneous order (R. Eyde, personal communication). On cytological grounds, Cornales ($x = 13$) appear distinct from Umbellales ($x = 6$), with which they were combined by Thorne (1968) and Takhtajan (1969); however, the orders are probably more closely related than is suggested by their wide separation in the system of Cronquist (1968).

V-7. *Santalales*.—Only six chromosome counts have been reported for Olacaceae, each for a separate genus; these indicate basic chromosome numbers of $x = 10, 12, 13$, and 19. The only count reported for Opiliaceae to date is $n = 10$. Santalaceae, which would amply repay further investigation, have $x = 5, 6, 10, 12, 13, 19$, and 36 in a very few scattered counts. Loranthaceae have $x = 12$ (Barlow & Wiens, 1971), with progressive aneuploid reduction, while Viscaceae have two groups, one with $x = 14$ and the other with $x = 10, 11, 12$, and 13 (Wiens & Barlow, 1971). Eremolepidaceae have $n = 13$ and $n = 10$ in the two available counts, each from a separate genus. In Balanophoraceae, one species each of the distantly related *Helosis* and *Thonningia* have $n = 18$, and one of *Balanophora* has $n = \text{ca. } 16$; if the family is really heterogeneous and the result of convergent evolution (Airy Shaw, 1966), further cytological information would be highly desirable. The only count of Cynomoriaceae, made in 1903, was $n = 12$. No chromosome counts are available for Dipentodontaceae, Grubbiaceae, Medusandraceae, or Myzodendraceae. For the order as a whole, much more information is needed, particularly on Santalaceae, to determine whether chromosome numbers of $n = 5$ (*Santalum*) and $n = 6$ (*Thesium*) were derived by aneuploid reduction or reflect the original basic chromosome number for the family and order. At present, $x = 6$ might cautiously be advanced as the original basic chromosome number of the group, with $x = 12$ and $x = 18$ important polyploid derivatives.

V-8. *Rafflesiales*.—For Rafflesiaceae, $x = 12, 10$, and perhaps 8 ($n = 16$ in *Cytinus hypocistis* L.). *Mitrastemon*, treated by Cronquist (1968) as a distinct family, also has $x = 10$. Hydnoraceae have not been studied cytologically.

V-9. *Celastrales*.—Hippocrateaceae have $x = 14$, with $n = 30$ in *Hemiangium* (Bawa, 1973). Celastraceae, for which only 9 of 55 genera have been examined, have $x = 9, 8, 10, 14$, and 12 as important chromosome numbers; they should certainly be studied much more extensively cytologically. *Stackhousia* (Stackhousiaceae) has $x = 9$ and 10. The only count available for Salvadoraceae is $n = 12$. *Ilex*, the only one of the three genera of Aquifoliaceae for which information is available, has $x = 20$ (Frierson, 1959; F. S. Santamour, Jr., personal com-

munication). In four Himalayan species, $n = 18$, although most species from this region, like those from other areas, have $n = 20$ (Mehra & Khosla, 1969). Icacinaceae, for which counts are available for six of about 58 genera and seven of about 400 species, have $x = 10$ in four genera, and $n = 11$ and $n = 12$ in one each. Dichapetalaceae evidently have $n = 12$ (Gadella, 1972), based on counts from *Dichapetalum* only. No information is available concerning Geissolomataceae, Siphonodontaceae (Capusiaceae), or Cardiopterygaceae. Corynocarpaceae fit better here cytologically (Takhtajan, 1969) than in Ranunculales (Cronquist, 1968). If Celastrales constitute a homogeneous and monophyletic group, then the original basic chromosome number is likely to be $x = 12$, with early and important aneuploid reduction. As a close relationship with Santalales seems likely (Thorne, 1968, combines the orders), the meaning of $x = 6$ in Santalaceae assumes importance in understanding the evolution of the entire complex.

V-10. *Euphorbiales*.—Buxaceae have $x = 14$ (*Buxus*, *Sarcococca*), $x = 10$ (*Notobuxus*), $n = 13$, 27 (*Pachysandra*; G. Davidse, personal communication), and $x = 13$ (*Simmondsia*). Unfortunately, no count is available for *Styloceras*, the remaining genus, which has been grouped with *Notobuxus* in a tribe Stylocereae. For Euphorbiaceae, much more information is needed; fewer than 5 per cent of the approximately 7,000 species have been examined cytologically. Nevertheless, in the subfamily Phyllanthoideae, with $x = 13$ in the more primitive taxa (Webster, 1967), it seems highly likely that this is the original basic chromosome number. In the other and more diverse subfamily, Euphorbioideae (Crotonoideae) $x = 9$, 10, and 11 are the most frequent basic numbers, with the latter perhaps the most likely candidate for the original basic chromosome number, based on present evidence (G. L. Webster, personal communication). Despite the arguments of Hans (1973), there seems to be little basis for accepting $n = 7$ as one of the original basic chromosome numbers of Euphorbiaceae on present evidence. No information is available for the very distinct Australasian genera *Poranthera* and *Ricinocarpos* (Airy Shaw, 1966). Daphniphyllaceae have $n = 16$ (two species). For Pandaceae, only one count for *Microdesmis*, $n = 15$, is available; this number is unusual in Euphorbiaceae (Webster, 1967), and it would be interesting to have a determination of chromosome number for *Panda*. The monotypic Chilean Aextoxicaceae have not been examined cytologically. Webster (1967) considers the similarities between Euphorbiaceae and Buxaceae to be the result of convergent evolution, but chromosomal evidence provides a weak suggestion of $x = 7$ (or 14) in both. This is also an important basic chromosome number in Malvales and Urticales, related to Euphorbiales by Thorne (1968) and many other authors, but widely separated by Cronquist (1968).

V-11. *Rhamnales*.—Rhamnaceae have $x = 12$, with $x = 11$ in the tribe Colletieae and some aneuploidy in *Rhamnus*, sensu lato. The very distinct monotypic African *Maesopsis*, constituting a subfamily of its own, has $n = 9$, as does the only species of *Gouania* to be counted to date; their relationships should be studied further. Leeaceae, a monogeneric family, have $x = 12$, with one report of $n = 11$, and one of $n = 10$. Vitaceae have $x = 12$ with aneuploidy in *Cissus*, $x = 11$ and 13 in *Tetrastigma*, $x = 10$ in *Cayratia*, and $x = 20$ or 19 in other genera. The original basic chromosome number for this family, and for the whole order,

seems probably to be $x = 12$. Cytologically, these three families are similar, which accords with their long-assumed relationship (Takhtajan, 1969). They are widely separated by Thorne (1968), who allies the Rhamnaceae with a series of orders in which $x = 7$, and Vitaceae with Cornales in which $x = 11$.

V-12. *Sapindales*.—Staphyleaceae have $x = 13$, Melianthaceae $x = 19$ (18 also?), Greyiaceae $x = 17$ or 16 (Goldblatt, 1976a). Connaraceae have $n = 14$ in one count each for six genera and $n = 13$ in one count for a seventh genus, a pattern that would fit equally well here or in Rosales (Thorne, 1968; Takhtajan, 1969, as an order near Rosales). Sapindaceae, which will prove very interesting cytologically when better sampled, have basic numbers of $x = 11, 12, 13$ (Mehra & Khosla, 1969), 14, 15, and 16 in 23 of some 150 genera that have been examined. For the widespread *Dodonaea viscosa* Jacq., counts of $n = 14, 15$, and 16 have been reported. Hippocastanaceae are sharply distinct cytologically, with $x = 20$ in both genera. Aceraceae have $x = 13$. Burseraceae probably also have $x = 13$, with $n = 11$ and 12 the only two chromosome numbers reported for *Bursera*. In *Dacryodes*, the only count reported to date is $n = 23$. In Anacardiaceae, $x = 14, 15$, and 16 are common basic numbers, with $x = 12$ represented in several genera. *Mangifera* has $n = 20$, also reported for *Lannea* (another species has $n = 14$), and *Anacardium* seems to have $n = 21$. Both genera of Podoaceae, *Campylopetalum* and *Dobinea* (Mehra & Khosla, 1969), have $n = 7$, which strongly supports their segregation from Anacardiaceae as a distinct family. It seems justifiable, however, to conclude that $x = 7$ is the original basic chromosome number for Anacardiaceae, with most of the evolution proceeding at the tetraploid level. Simaroubaceae have $x = 14, 13$, and 12 commonly, with the first perhaps the original basic chromosome number. Rutaceae were considered by Smith-White (1959) to have an original basic chromosome number of $x = 9$, which stands in sharp contrast to all other Sapindales. Ehrendorfer (in press) in contrast, considers that $x = 9$ was derived by aneuploid increase from $n = 7$ early in the evolution of the family, and that its original base number is $x = 7$. Cneoraceae have $n = 18$. For Meliaceae (Styles & Vosa, 1971), $x = 14, 13$ (Mehra et al., 1972), and 12 are perhaps the lowest numbers determined with certainty, but $n = 8$ and 11 have been reported for two different species of *Sandoricum*, which should be studied in more detail. The single species that has been segregated as Aitoniaceae, *Nymanina capensis* (Thunberg) S. O. Lindberg, has $n = \text{ca. } 24$ (Goldblatt, 1976a). Zygophyllaceae have $x = 13$, judging from the distribution of this chromosome number in relatively primitive, woody genera, with descending aneuploidy in a number of genera, culminating in a base number of $x = 6$ in the advanced genus *Tribulus* (D. M. Porter, personal communication). Cytologically, Coriariaceae ($x = 20$) fit much better here, where they are placed by Takhtajan (1969), than in Ranunculales (Cronquist, 1968). They are equally compatible with Rosales (Thorne, 1968). Summing up for Sapindales, $x = 7$, with early evolution of $x = 14$ and, from it, $x = 13$, as well as (in Rutaceae and Cneoraceae) $x = 9$. No information is available concerning Akaniaceae, Julianaceae, Stylobasiaceae, or Surianaceae.

V-13. *Geraniales*.—Within Oxalidaceae, the rather isolated, woody genus *Averrhoa* has $x = 12$ and 11. Amongst the herbaceous members of the family, $x = 9$ in *Biophytum*, and *Oxalis* has every gametic chromosome number from

$n = 5$ to $n = 12$ inclusive, with a mode at $n = 7$. Such a pattern would be consistent with an original basic chromosome number for the family of $x = 12$, with aneuploid reduction in the herbaceous groups, or with an original basic number of $x = 7$, with subsequent polyploidy and aneuploid change. The two genera of Geraniaceae with the least specialized flowers, *Sarcocaulon* and *Monsonia*, have $n = 22$ and $n = 12$ respectively, whereas *Erodium* may have $x = 10$ and *Geranium* $x = 14$. The most specialized genus, *Pelargonium*, has $x = 11$. *Balbisia*, one of the genera sometimes segregated as Ledocarpaceae, has $n = 9$. Limnanthaceae all have $n = 5$. Tropaeolaceae have $x = 14$, 13, and 12. Balsaminaceae consist of *Hydrocera*, possibly the more primitive genus, with $n = 8$, and *Impatiens* with $n = 6$ –11 inclusive, the most common numbers being $n = 10$, 8, and 7 (Jones & Smith, 1966). For the order as a whole, it is almost impossible to guess whether the original basic chromosome number is $x = 7$, 12, or 14.

V-14. *Linales*.—For Erythroxylaceae, $n = 12$. The only determination of chromosome number available for Humiriaceae is likewise $n = 12$. In Linaceae, $n = 11$ and 10 in *Reinwardtia*; $x = 9$ in *Linum* (Harris, 1968), with aneuploid reduction to $n = 6$ in some species; $n = 18$ and 17 in *Hesperolinon*, and $x = 6$ in *Hugonia*. The last mentioned may indicate an original basic chromosome number of $x = 6$ for the order Linales as a whole.

V-15. *Polygalales*.—Only 35 chromosome counts, representing 12 genera, appear to be available for Malpighiaceae, a family of about 60 genera and 800 species. In *Galphimia* and *Lophanthera* $x = 6$, which implies that the numbers $x = 12$, 11, 10, and 9 are derived from it by polyploidy followed by aneuploid reduction, and that $x = 6$ is the basic chromosome number for the family. Polygalaceae have all gametic chromosome numbers from $n = 7$ to $n = 12$ in different genera, and in *Polygala* itself $n = 8$, 12, and 14–21 inclusive. In *Monnina*, $x = 5$. There seems to be no point in attempting to guess a basic chromosome number with the available information. Krameriaceae have $x = 6$. No information about the chromosomes of Trigoniaceae, Vochysiaceae, Tremandraceae, Xanthophyllaceae, or Polygalaceae tribe Moutabeae seems to have been published. For the order, $x = 6$ seems to be the original basic chromosome number, with some doubt as to the course of evolution in Polygalaceae.

V-16. *Umbellales*.—Araliaceae clearly have $x = 12$. *Helwingia*, placed here for example by Hutchinson (1959), has $x = 19$ and is very distinct cytologically. In Apiaceae, Apioideae have $x = 11$, with frequent descending aneuploidy, whereas Hydrocotyloideae and Saniculoideae have $x = 8$. It is possible that *Oreomyrrhis* (Mathias & Constance, 1955), one of the most distinct of the Apioideae, with $n = 6$ (one species has $n = 7$), retains the basic chromosome number of the order. For the order as a whole, I cautiously postulate a base number of $x = 6$, especially in view of the very close relationship between Apiaceae and Araliaceae (Thorne, 1973).

VI. SUBCLASS ASTERIDAE

VI-1. *Gentianales*.—In families that have been segregated from Loganiaceae, Antoniaceae and Strychnaceae have $x = 11$, Desfontainiaceae $n = 7$. Spigeliaceae

have $n = 10$ in *Cynoctonum*, $x = 8$ and 13 in *Spigelia*. Potaliaceae evidently have $x = 6$ in *Fagraea* and *Anthocleista* ($n = 24$ and $n = 30$ are the two reported numbers). In Loganiaceae, sensu stricto, $x = 11$, 10 , and 8 are the basic chromosome numbers. In *Retzia*, probably most closely related to Loganiaceae, $n = 12$ (Goldblatt & Keating, 1976). In Gentianaceae, $x = 10$, 11 , and 13 are the most common basic numbers, with aneuploid numbers below $n = 10$ having evidently been derived independently in several different lines. Both $x = 10$ and $x = 13$ occur, with other aneuploid numbers both in *Gentiana*, sensu stricto, and in *Swertia*. In the Brazilian *Deianira*, the only member of the South American tribe Helieae to be examined cytologically, $n = 7$, suggesting $x = 7$ for the family, with tetraploidy occurring early in its evolution. Apocynaceae have $x = 11$, with rather frequent descending aneuploidy in a number of lines to $n = 6$. Asclepiadaceae also have $x = 11$, but with aneuploidy much less common; a very high proportion of the species examined have had $n = 11$. The basic chromosome number for the order is probably $x = 7$, which seems to have given rise to $x = 6$ early in the history of the group. Presumably, $x = 11$ in Antoniaceae, Strychnaceae, and Apocynaceae-Asclepiadaceae have been derived independently from $x = 14$.

VI-2. *Polemoniales*.—Nolanaceae have $n = 12$. Solanaceae also have $x = 12$ with a good deal of aneuploid reduction in different lines, reaching $n = 7$ in *Petunia*. The original basic number of Convolvaceae may be $x = 7$, judging from its presence, together with $x = 14$ and $x = 15$, in *Cuscuta*; these latter two numbers are the most common in the family, suggesting perhaps the early presence of $n = 7$ and $n = 8$ and subsequent aneuploid reduction at the tetraploid level in the ancestors of *Porana* ($x = 13$), *Evolvulus* ($x = 13, 12$), *Calystegia* ($x = 11$), and within *Convolvulus* sensu stricto ($x = 15, 14, 12, 11, 10$) and *Merremia* ($x = 15, 14, 11$). Menyanthaceae have $x = 9$, and seem to fit better in this order cytologically than in Gentianales (Takhtajan, 1969). Polemoniaceae also have $x = 9$ (Grant, 1959). Hydrophyllaceae might also have a basic chromosome number of $x = 9$, if both aneuploid increase and decrease are assumed; this number does occur in several key groups, and the South African *Codon* has $n = 17$ ($9 + 8?$). Aneuploid increase would then be involved in the evolution of the *Phacelia magellanica* group, the miltitzoid phacelias, *Ellisia*, *Eucrypta*, *Romanzoffia*, and *Codon*, with polyploidy involved in the origin of *Turricula* ($n = 13$) and *Eriodictyon* ($n = 14$). Lennoaceae have $x = 9$ also. If this order is a monophyletic one, $x = 7$ is probably the original basic chromosome number, with aneuploid reduction at that level or from the tetraploid $n = 14$ to give rise to $x = 12$, early in the history of the group.

VI-3. *Lamiales*.—The original basic chromosome number of Boraginaceae seems to be $x = 12$, with aneuploid reduction very frequent and reaching $n = 4$ in *Arnebia* and one species of *Amsinckia*. Important basic numbers in Ehretioideae are $x = 10, 9$, and 8 , with $n = 16, 15, 14, 24$, and possibly 21 represented in *Cordia* (Bawa, 1973). *Callitriche* (Callitrichaceae) has species with $n = 3, 4, 5, 10$ and higher numbers; $x = 5$ appears probable. Verbenaceae seem to have been insufficiently studied cytologically to make speculations about their original basic chromosome number profitable. The basic numbers $x = 7$ in *Verbena* sensu stricto, $x = 5$ in *Glandularia*, and the report of $n = 6$ in *Priva lappulacea* (L.) Pers.

almost certainly represent reductions. Otherwise, the only report of a chromosome number less than $n = 11$ in Verbenaceae is one of $n = 9$ for *Phyla nodiflora* (L.) Greene. On the other hand, numbers such as $n = 11, 12, 13, 14, 15, 16, 17$, and 18 are well distributed among the genera for which information is available, with evident aneuploid change in such genera as *Callicarpa* ($x = 16, 17, 18$), *Gmelinia* ($x = 18, 19, 20$), and *Vitex* ($x = 12, 13, 15, 16, 17$). *Nyctanthes*, a very distinctive genus usually included in Verbenaceae, has $n = 23$ like many genera of Oleaceae, another family with which it has been allied. Kundu & De (1968) have concluded that it may best be recognized as a distinct family near Oleaceae. The monotypic Phrymaceae have $n = 14$, although Sugiura (1936) has been misquoted as having reported $n = 7$, which he did not.

In the large family Lamiaceae, counts are available for nearly half of the 180 genera, but only a very low proportion of the 3500 species. With the help of Briquet's (1895) invaluable treatment, some order may be brought out of the rich diversity of chromosome numbers reported to date. In the clearly most primitive subfamily Ajugoideae, $x = 14$, the most common basic number in *Ajuga*, may be the basic number, although $n = 16$ and $n = 31$ are also represented in the genus; for other genera of the subfamily that have been examined cytologically, $x = 13$ in *Amethystea*; $x = 12$ in *Rosmarinus*; $x = 10$ in *Trichostema*, with subsequent aneuploid reduction in the annuals to $x = 7$ (Lewis, 1960); $x = 9$ in *Teucrium*; and $x = 16$ ($= 8?$) in *Tunnea*. Much aneuploid reduction in chromosome number has taken place in the more advanced subfamily Ocimoideae, with reduction to $x = 7$ in three separate tribes, and in Stachyoideae, also with reduced chromosome numbers in three tribes. The Nepeteae will serve to illustrate these reductions; in *Agastache*, *Meehania*, and *Glechoma*, $x = 9$; in *Nepeta*, $x = 9$ and 8 ; in *Lallemantia*, $x = 7$; in *Schizonepeta*, $x = 6$; and in *Dracocephalum*, $x = 7, 6$, and 5 — $n = 5$ in this genus being the lowest chromosome number yet recorded in the family. Unfortunately, no chromosome counts seem to be available for the primitive Australian subfamily Prostantheroideae, which will be helpful in testing the hypothesis of $x = 14$ as the original basic chromosome number for the family Lamiaceae. The original basic chromosome number of Lamiales might also be $x = 14$, with reduction to $x = 12$ in the ancestor of Boraginaceae.

VI-4. *Plantaginales*.—Plantaginaceae, the only family, seem clearly to have $x = 6$.

VI-5. *Schrophulariales*.—Buddlejaceae have $x = 19$, which accords with their distinctiveness from Loganiaceae. Oleaceae (Johnson, 1957) have $x = 11$ (*Menodora*) and $x = 13$ (*Jasminum*) in the tribe Jasmineae; $x = 13$ in *Fontanesia*, the only genus of Fontanesieae; and $x = 14$ in both genera of Forsythieae. These tribes belong to the subfamily Jasminoideae. In the other subfamily, Oleoideae (including Schrebereae; Briggs, 1970), $x = 23$ with aneuploidy in *Syringa*, *Osmanthus*, and *Phillyrea*, and $n = 20$ the only chromosome number reported for *Haenianthus* (Nevling, 1969). Two African species of the closely related *Linociera* also have $n = 20$, a chromosome number otherwise unknown in the family, whereas two species from New Caledonia have $n = 23$. This suggests that African species of *Linociera* may have had a common ancestor with *Haenianthus*. As suggested by Taylor (1945), $x = 14$ is probably the original base number in

Oleaceae, with $x = 23$ formed following aneuploid reduction to $n = 12$ and $n = 11$. Chromosome counts of the remaining unexamined members of Jasminoideae, *Comoranthus*, *Noldeanthus*, and especially *Myxopyrum*, would be especially interesting.

Scrophulariaceae are extremely diverse cytologically, and the overall pattern is difficult to determine. Many of the tribes appear to be characterized by descending aneuploidy, but it is not certain whether any of the original diploids persist in most of them or not. For example, in Digitaleae, $x = 14$ would appear reasonable, but the monotypic European *Erinus* has $n = 7$; in Cheloneae, $x = 14$ also appears reasonable, but *Collinsia*, perhaps an advanced genus, has $x = 7$; in Rhinanthaeae, $x = 12$ seems reasonable, but there is a doubtful report of $n = 6$ for *Bartsia alpina* L., which otherwise has reports of $n = 12$, $n = 14$, and $n = 18$; and in Gratioleae, *Gratiola* and *Lindernia* could be interpreted as having descending aneuploid series to $n = 7$, but the only species of *Dopatrium* examined has $n = 7$ also. Hemimerideae seem to have $x = 14$, 12, 10, and 9, and Verbasceae, with rotate corollas, have an inferred $x = 10$, 9, and 8. Perhaps the most important clue comes from the very distinct South African Selagineae, which have even been segregated as a distinct family; both species counted, in two different genera, have $n = 7$. This group has been added to Globulariaceae, which have $x = 8$, by Cronquist (1968), and both are related to Scrophulariaceae-Manuleae, which have $x = 6$. On the balance, $x = 7$ is assumed to be the original basic chromosome number for Scrophulariaceae.

Myoporaceae have $x = 9$, based on $n = 54$ in *Myoporum laetum* Forst. f. and $n = 18$, 36, and 54 in *Eremophila*. Globulariaceae have $x = 8$.

Despite information on about half of the approximately 120 genera, it is difficult to postulate an original basic chromosome number for Gesneriaceae (Moore & Lee, 1967; Ratter, 1975). Considering the mainly New World subfamily Gesnerioideae first, $x = 9$ is probable for the Columneae, which have a superior ovary and both terrestrial and epiphytic habits, and some of the apparently more advanced genera have $x = 8$ (H. E. Moore, Jr., personal communication). In the epiphytic Gesnerieae, $x = 7$, with $n = 7$ recently reported for *Gesneria sintenisii* Urb. (Nevling, 1969). In other tribes, $x = 13$ and 11 are frequent, $x = 12$ and 10 less so. The interpretation of $n = 16$ in *Besleria* is not clear at present, but it is perhaps tetraploid based on $x = 8$. In the mainly Old World subfamily Cyrtandroideae, $x = 10$ is found in certain genera of Cyrtandreae, Klugieae, and Didymocarpeae (Burt, 1962), with $x = 8$, 9 and apparent multiples widespread in all four tribes. The numbers $n = 8$, 9 and apparent multiples widespread in all four tribes. The numbers $n = 8$ and 9 are likewise represented in the large genera *Chirita*, *Didymocarpus*, and *Boea*, which have various aneuploid and polyploid derivatives also. In summary, $x = 9$ may be the original basic chromosome number for Gesnerioideae and $x = 8$ or 9 for Cyrtandroideae (B. L. Burt, personal communication; Ratter, 1975). This suggests $x = 9$ as the original basic chromosome number for the family, particularly if the two subfamilies are actually directly related to one another.

Orobanchaceae have $x = 12$ and 19 in *Orobanche* and $x = 18$, 19, 20, and 21 in some other genera; a very tentative suggestion of $x = 7$ for the family might be

deduced from these numbers. In Bignoniaceae, $x = 20$ is by far the most frequent base number in all tribes, and the only one known in the less diverse tribes Crescentieae and Tourrettieae. Significantly, *Oroxylum*, the only one of the presumably most primitive genera of the family (those with five fertile stamens) which has been counted, has $n = 14$ ($n = 15$ also reported), which, taken together with the frequent occurrence of $n = 20$, suggests $x = 7$ as basic to the family. *Millingtonia* has $n = 15$, but most other chromosome counts deviating from $n = 20$ should be reconfirmed. The most derived herbaceous genera, however, have some of the lowest chromosome numbers ($n = 11$ in *Incarvillea*, $n = 15$ in *Argylia*), which might be derived by aneuploidy at the tetraploid level. In Acanthaceae, the relatively few chromosome counts that have been made reveal a great diversity; $x = 14$ and $x = 21$ are frequent, as are other basic numbers from $x = 8$ to $x = 17$. On the basis of very limited evidence, $x = 7$ is suggested as the original basic chromosome number for Acanthaceae, as tentatively proposed by Grant (1955). In Pedaliaceae, sensu stricto, $x = 8$ and 13, and in Martyniaceae, $x = 15$ and 16. Lentibulariaceae have $x = 11$, 8, and (in one species) 6 in *Pinguicula*; $x = 6$, 7, 9, 10, 14, 15, 18, and 21 in *Utricularia*; and $n = 9$ in *Orchyllium*. Hydrostachyaceae are known only from a 1915 count of $2n = 20-24$. For Scrophulariales as a whole, $x = 7$ seems possible, although much work remains to be done, and the original basic chromosome number might also have been $x = 8$, 9, or 10. Oleaceae and Buddlejaceae have had polyploid origins.

VI-6. *Campanulales*.—Sphenocleaceae have $n = 12$. In Campanulaceae, $x = 7$ in the subfamily Lobelioideae, with only a few deviating counts, but considerable aneuploidy in *Downingia*. The subfamily Campanuloideae exhibits considerable cytological diversity, with $x = 7$ still probably the original basic chromosome number. In *Campanula*, a large and diverse genus with many satellite genera, gametic chromosome numbers of $n = 7-12$ inclusive, as well as $n = 14$, 15, and 17, with various multiples, occur. In *Phyteuma*, $n = 10-14$ and 17 occur. Several genera related to *Campanula* have $x = 17$, and it eventually should be possible to work out the chromosomal phylogeny of the group in elegant detail. Even though *Specularia* has $x = 7$, 8, and 10, and *Peracarpa* has $n = 15$, it is likely that most chromosome numbers in the subtribe Campanulinae (all genera mentioned thus far) between $n = 8$ and $n = 13$ have been derived by aneuploid reduction from $n = 14$. In the Cyphioideae, *Nemacladus* has $x = 9$ (W. L. Bloom, personal communication). The two counts available for Stylidiaceae, each from a different genus, have been $n = 15$. The monotypic Australian Brunoniaceae have $x = 9$. Goodeniaceae, another mainly Australian family, have $x = 8$ in six genera; $x = 9$ in three, including *Leschenaultia*, *Dampiera*, and *Anthotium*; and $x = 7$ in three species of *Goodenia*, which otherwise has $x = 8$. Peacock (1963) considered it impossible to say whether $x = 8$ or 9 was the original basic number, but stated that $x = 7$ was clearly derived from $x = 8$. Cytologically, Brunoniaceae and Goodeniaceae do not seem closely related to Campanulaceae or Stylidiaceae, which would be in agreement with the observations of Carolin (1960).

VI-7. *Rubiales*.—As summarized by Verdcourt (1958), the cytological information available concerning Rubiaceae suggests that $x = 11$ is the original basic chromosome number, with reduction in several lines. On the other hand, the

presence of $x = 14$ in the morphologically advanced Spermacoceae and of $x = 12$ in *Catesbaea*, *Hamelia*, and *Hoffmannia*, not primitive genera, suggests aneuploid increase. Cytologically, the family would fit well in Gentianales, where it is placed by Thorne (1968) and Takhtajan (1969). The evidence would also agree well with a derivation of Rubiaceae from Loganiaceae (Cronquist, 1968: 87).

VI-8. *Dipsacales*.—Caprifoliaceae have $x = 9$ with $x = 8$ in some genera. Adoxaceae have $n = 18$ and possibly higher polyploid numbers in the single species. Valerianaceae have $x = 8$, but with $n = 11$ in *Patrinia*, one of the two genera with four stamens; the relationship of this number to $x = 8$ remains to be determined. In *Valeriana* in which $x = 8$ predominates, two species have $n = 12$. Dipsacaceae have $x = 9$ (Ehrendorfer, 1964), with much aneuploid reduction in the evolution of various genera. Calyceraceae have not been well sampled, but have $n = 8, 15, 18$, and 21 in the counts reported so far. For the order as a whole, $x = 9$ without much doubt.

VI-9. *Asterales*.—Asteraceae have $x = 9$ (e.g., Stebbins et al., 1953; Raven et al., 1960; Raven & Kyhos, 1961; Solbrig et al., 1964) with a great deal of aneuploidy and polyploidy.

CLASS LILIOPSIDA (MONOCOTYLEDONEAE)

I. SUBCLASS ALISMATIDAE

I-1. *Alismatales*.—Limnocharitaceae have $x = 10, 8$, and 7 in different genera, whereas the monotypic Butomaceae have $x = 13$. In Alismataceae, $x = 7$ and 11 are both important basic numbers.

I-2. *Hydrocharitales*.—Hydrocharitaceae have $x = 8, 7$, and 11 as frequent basic numbers, with considerable aneuploidy indicated by the published reports.

I-3. *Najadales*.—Aponogetonaceae have $x = 8$, the ditypic Scheuchzeriaceae $n = 11$, Juncaginaceae $x = 6$ (including *Lilaea*), Najadaceae $x = 6$, Potamogetonaceae $x = 7$ and $x = 13$, Ruppiaceae $x = 10$, Zannichelliaceae $x = 6$, and Zosteraceae $x = 6$ and 7 .

I-4. *Triuridales*.—Counts of $n = 14, 22$, and 24 have been reported for different species of *Sciaphila* (Triuridaceae); no information is available for Petrosaviaceae.

II. SUBCLASS COMMELINIDAE

II-1. *Commelinales*.—The only count available for Rapateaceae is for the single African species, *Maschalocephalus dinklagei* Gilg & K. Schum., $n = 11$. *Xyris* (Xyridaceae) has $n = 9$ (North American species), 13 (six Australian species), and 17 (one Asian, one African species), with a dubious 1914 report of $n = 16$. Mayacaceae are unknown cytologically. Commelinaceae (Jones & Jopling, 1972) have an exceptionally wide range of chromosome morphology, and have basic chromosome numbers ranging from $x = 4$ to $x = 20$. In the Old World and pantropical genera, $x = 8$ and $x = 9$ are frequent base numbers, whereas in the New World genera, $x = 6$ and $x = 8$ are common. No original basic chromosome number or satisfactory scheme for chromosomal evolution in the family has been proposed.

II-2. *Eriocaulales*.—For *Eriocaulon*, $x = 8$ is the more common basic number, but $n = 10$ occurs in *E. compressum* Lam. No other genus of Eriocaulaceae has been examined cytologically.

II-3. *Restionales*.—*Flagellaria* (Flagellariaceae) has $n = 19$ (three species). In the Australasian members of the Restionaceae, $x = 6$ or 12 and $x = 11$ are frequent, with $x = 13$, 9, 7, and 16 also represented. As $x = 11$ and $x = 7$ are important basic chromosome numbers, at least among the Australian species of the family (Briggs, 1963) and since $x = 12$ and $x = 6$ occur in several genera that are not closely related (Briggs, 1966, personal communication), it is tentatively suggested that either $x = 6$ or 7 might be the original basic chromosome number for the family, with early tetraploidy followed by aneuploid reduction. On the other hand, *Hypodiscus aristatus* Nees, the only African species of the family for which chromosomal information is available, has $n = 16$ (Krupko, 1962), and further studies are clearly necessary. *Anarthria*, segregated by Cronquist (1968) as a separate family, has $x = 11$ and fits in cytologically with the rest of Restionaceae, whereas no information is available concerning Ecdeiocoleaceae. Centrolepidaceae, poorly sampled, have $n = 13$ and 10. For the order, $x = 7$ could be considered a likely candidate as the original basic chromosome number.

II-4. *Juncales*.—For *Luzula*, $x = 6$, and for *Juncus*, $x = 20$, with descending aneuploidy in some specialized groups. The very low number $n = 3$ in *Luzula* must clearly be derived also. They are the only genera of Juncaceae examined cytologically. Thurniaceae are unknown in this respect.

II-5. *Cyperales*.—At least some genera of Cyperaceae have polycentric chromosomes, and all numbers from $n = 5$ to 20 and above are represented in one or more species. The chromosomal situation in this family is similar to that in *Juncus*. Poaceae have $x = 12$, judging from the prevalence of this number among Bambuseae, if the scattered morphologically advanced genera with $x = 6$ in other tribes have been derived by aneuploid reduction, as appears probable. The interpretation of $x = 7$ in festucoid tribes (Brown & Smith, 1972) is problematical, but this number has in all likelihood been achieved by aneuploid reduction.

II-6. *Typhales*.—Both Typhaceae and Sparganiaceae have $x = 15$.

II-7. *Bromeliales*.—Marchant (1967) found $x = 25$ to be characteristic of most Bromeliaceae. *Cryptanthus* has $x = 17$, earlier reports of $x = 18$ evidently being in error. In *Aechmea tillandsioides* (Mart. ex Schult. f.) Baker, Marchant (1967) found $n = 21$, and suggested that it might have arisen through a combination of $n = 25$ and $n = 17$ at some early date. Subsequently, Sharma & Ghosh (1971) have reported $n = 23$, 24, 26, 27, and 49 in various members of the family and $n = 18$ in addition to $n = 17$ in *Cryptanthus*; all such records need careful evaluation and reconfirmation.

II-8. *Zingiberales*.—In Strelitziaceae, *Ravenala* and *Strelitzia* both have $n = 11$, with most species of the latter having $n = 7$. Both species of Lowiaceae have been examined cytologically, and had $n = 9$. *Heliconia*, only genus of Heliconiaceae, has $n = 12$ and $n = 11$ and, should they be confirmed, other chromosome numbers derived from them. Musaceae have $n = 9$, 10, and 11 as equally feasible candidates for original basic chromosome number (Simmonds, 1962). Costaceae have $x = 9$. Zingiberaceae have $x = 11$ and 12 as important basic chromosome numbers, but

also $n = 10$ (*Caulokaempferia*), and $x = 13, 14, 16, 17$, as well as higher numbers, in other genera. Cannaceae have $x = 9$. Marantaceae have $x = 11, 12, 13$, and 14 , as well as $x = 4, 6, 8, 9$, and 10 , as common basic numbers. Looking at the order as a whole, it is most likely that $x = 11$ could have been the original basic number (Mahanty, 1970).

III. SUBCLASS ARECIDAE

III-1. *Arecales*.—Arecaceae apparently have an original basic chromosome number of $n = 18$ (Moore & Uhl, 1973; R. W. Read, personal communication), judged from its presence in coryphoid, phenicoid, and some genera of arecoid and borassoid palms. Reduced chromosome numbers are found in a number of lines, with $n = 17$ occurring widely, and $n = 16, 14$, and 13 also represented.

III-2. *Cyclanthales*.—In the three species of *Carludovica* that have been studied cytologically, $n = 9, 15$, and 16 occur, suggesting that further studies may be very interesting.

III-3. *Pandanales*.—The basic chromosome number is clearly $x = 30$, with some aneuploidy. This would be in agreement with the notion of a relationship with Typhales, as indicated by the arrangements of Takhtajan (1969) and to some extent Thorne (1968).

III-4. *Arales*.—In Araceae, the preponderance of species with $n = 14$ and 21 , coupled with other important base numbers such as $x = 13$ and 12 , suggests $x = 7$ as the original basic chromosome number. There is, however, no species of the family with $n = 7$. As far as known, Lemnaceae have $n = 15, 20, 21, 22, 25, 28-30, 35$, and 40 ; the first four numbers might be consistent with a hexaploid origin on $x = 7$. *Pistia*, the genus of Araceae often cited as transitional to Lemnaceae, has $n = 14$.

IV. SUBCLASS LILIIDAE

IV-1. *Liliales*.—Philydraceae have $n = 8$ and $n = 17$. Pontederiaceae have $x = 8$ (*Pontederia*, *Eichhornia*) and 7 (*Monochoria*; also $n = 20$ and 26), as well as 15 (*Heteranthera*). For the large complex of genera and tribes treated by Cronquist (1968), Thorne (1968), and others as Liliaceae, cytological information has been extremely useful in the grouping of genera into suprageneric taxa. For example, the grouping of *Yucca* and *Agave*, originally placed in separate families but with an utterly distinctive gametic chromosome complement consisting of 5 large and 25 small chromosomes, has become a classical example of the use of cytological data in higher classification (McKelvey & Sax, 1933). The extension of this pattern to other genera, however, becomes more and more ambiguous (Darlington, 1956: 96-100), leading to doubts about the constitution of the family Agavaceae (Cronquist, 1968: 358), and even its abandonment owing to uncertainty about limits (Thorne, 1968). When available chromosomal information on *Liliaceae*, in the broad sense, is arranged according to the small and therefore presumably more or less natural tribes of Hutchinson (1959), no obvious original basic chromosome number emerges for the group as a whole, although all basic numbers from $x = 7$ to $x = 11$ are well represented. The general observation may be made that the tribes traditionally considered as Amaryllidaceae appear to have

an original basic chromosome number of $x = 12$ (or possibly 11), with reduction to $x = 7$ in Narcisseae, and that the Allieae, with $x = 9, 8, 7, 6$, and Agapantheae, with $x = 6$ and 15, appear slightly discordant in this group, where they have been placed by Hutchinson. What is known about the cytology of Iridaceae does not readily suggest an original basic chromosome number for the family (Goldblatt, 1971). It is of interest that Hutchinson's (1959) Hemerocalloideae, considered by him transitional to Amaryllidaceae, have basic chromosome numbers of $x = 11, 12$, and 14, like those of many Amaryllidaceae. Unfortunately, the critical tribes Isophysideae (Iridaceae) and Aphyllanthideae (Liliaceae) are unknown cytologically. Xanthorrhoeaceae have $n = 11$. Agavaceae have $x = 30, 19, 12$, and other basic numbers depending upon the composition of the group. Velloziaceae are known only from two 1925 counts of $n = 26$ and ca. 24 of the African *Talbotia elegans* Balfour, and from unpublished counts of $n = 9$ for *Vellozia* and $n = 16$ for *Barbacenia* (P. Goldblatt, personal communication) among the South American genera. Haemodoraceae have $n = 6, 8$, and 15, as well as $n = 7, 5$, and 4 (in *Conostylis*); no counts are available from the tribe Haemodoreae. Tecophilaeaceae, grouped by Cronquist (1968) with Haemodoraceae, have $x = 12$ and 10. Taccaceae have $n = 15$, based upon a single count. Stemonaceae have $n = 7$, also based upon a single count. Smilacaceae have $x = 13, 15$, and 16. Dioscoreaceae have $x = 10, 12, 13$, and 18. Both $n = 11$ and 12 have been reported for the same species of Cyanastraceae. Although chromosomal information will continue to be useful in the classification of suprageneric taxa in Liliales, it does not appear justifiable at present to attempt to deduce an original basic chromosome number for the order. Studies such as that of Huber (1969) will probably eventually point the way to a clarification of the evolutionary patterns in the group.

IV-2. *Orchidales*.—Although chromosomes will eventually prove useful in the classification of Orchidaceae (e.g., Jones, 1967), it would be premature to attempt to outline the pattern of evolution in the group or to suggest an original basic chromosome number. Burmanniaceae are very poorly known cytologically, with $x = 6$ a possible basic chromosome number based upon current information. Corsiaceae and Geosiridaceae are unknown cytologically.

DISCUSSION

A combination of chromosome number and morphology has proved useful in the classification of many families, as in the Rosaceae and Agavaceae discussed above. Another outstanding example is Gregory's (1941) study of Ranunculaceae, in which some genera have large chromosomes and $x = 8$; others small chromosomes and $x = 7$; and *Coptis* and *Xanthorrhiza* small chromosomes and $x = 9$. The cytological distinctiveness of *Paeonia*, with $x = 5$ and very large chromosomes, and of *Glaucidium* ($n = 10$) and *Hydrastis* ($n = 13$), with small chromosomes, was also demonstrated as a result of Gregory's pioneering study. Although Paeoniaceae is generally now recognized as a family only distantly related to Ranunculaceae, Hydrastiaceae generally are regarded as synonymous with Ranunculaceae. Cytological evidence favors their segregation.

In Onagraceae, Kurabayashi et al. (1962) demonstrated marked differences in the mitotic cycle of contraction in different tribes. Fuchsiaeae, Circaeaeae, and

Lopezieae have large, relatively undifferentiated, slowly contracting chromosomes; Onagreae medium-sized ones with presumably strongly contracted, heterochromatic segments near the centromeres; and Jussiaeae and Epilobieae small, tightly contracted ones that remained visible throughout interphase. Genera with the original basic chromosome number of the family, $x = 11$, occur in the first four of these tribes, with a considerable degree of aneuploid reduction in Lopezieae and Onagreae. Jussiaeae have $x = 8$, Epilobieae $x = 9, 10, 12, 13, 15, 16$, and 18 .

For the deduction of an original basic chromosome number in a family, a necessary step before comparisons can be made with other groups, a wide knowledge of phylogeny in the group is a necessary prerequisite. Outstanding studies that have analyzed complex situations and arrived at a solution to this problem include those of Johnson & Briggs (1963) on Proteaceae; those of Smith-White (1959) for various families; those of Barlow & Wiens (1971) on Loranaceae; Grant (1959) on Polemoniaceae; Walker (1971, 1972) on Annonaceae; and the classical studies of Sax (1931, 1933) on Rosaceae. For a number of families, including Commelinaceae (Jones & Jopling, 1972), Orchidaceae, Liliaceae, Dilleniaceae, Lythraceae, Melastomataceae, and Acanthaceae, deductions about the original basic chromosome number are premature. In many small families, on the other hand, the original basic chromosome number is obvious, as it is in families that are relatively uniform cytologically, such as Apocynaceae, Cactaceae, Magnoliaceae, and Araliaceae. Finally, in a number of families, the sort of detailed comparison of phylogeny with chromosomal information has not yet been made which would permit a truly critical evaluation of the original basic chromosome number but enough knowledge is available to permit a suggestion in this respect. Such suggestions have been made consistently in this paper so that they can be tested as more information about the plants concerned becomes available.

THE PATTERN IN MAGNOLIOPSIDA (DICOTYLEDONEAE)

A general review of the basic chromosome numbers and what they reveal about phylogeny in Cronquist's (1968) subclasses now seems in order. Darlington & Mather (1949: fig. 82; Darlington, 1956) attempted to provide a diagram of the relationships between basic chromosome numbers of woody dicots, but were hampered by many of the kinds of difficulties mentioned above. They accepted Hutchinson's (1959) phylogenetic relationships between the families.

I. *Magnoliidae*.—For this group, which has already been discussed in some detail, $x = 7$ is a plausible basic chromosome number at the ordinal level throughout. This would imply a basically tetraploid origin for Saururaceae and Piperaceae and could be used to argue for the exclusion of Coriariaceae and Corynocarpaceae from this line. It might also be used to argue for an ultimately tetraploid origin for Papaverales ($x = 10^?$), although the point cannot be settled with present evidence.

II. *Hamamelididae*.—The original basic chromosome number can logically be inferred to have been $x = 7$, although the great majority of the families are of polyploid origin. A common basic number is also $x = 7$, with $x = 20, 17, 16$ and perhaps also 19 and 15 represented. By analogy with Magnoliidae, $x = 12$, which

is also frequent, might have been derived by aneuploid reduction from $x = 14$, as seems clearly to have been the case in Fagales. The presence of $x = 12$ and $x = 16$ as the two basic chromosome numbers in Hamamelidaceae is anomalous and requires explanation. In Urticales, $x = 14$ was the original basic chromosome number but the group might better be moved to a position near Malvales in the dilleniid line. The presence of $x = 16$ in Leitneriales, Juglandales, and Myricales, which traditionally have been associated on morphological grounds, indicates that they may well have been derived from a common ancestor with this number. They are probably better referred to Rosidae, as implied by the classification of Thorne (1968). Polyploidy and aneuploid increase to $n = 8$ both seem to have been early events in the evolution of Hamamelididae. Similar trends seem to have occurred both in Hamamelidaceae and in Betulaceae.

III. *Caryophyllidae*.—The most important basic number is $x = 9$, presumably derived by aneuploid increase from $x = 7$ in the common ancestor of the group, as well as $x = 12$ and 11 in Basellaceae, $x = 11$ in Cactaceae, and $x = 14$ in Caryophyllaceae. Polygonales have $x = 10$, 11, or 12, which suggests reduction from $x = 14$ and might be taken as being in agreement with the suggestion that they are quite distinct from other Caryophyllidae. Plumbaginaceae probably have $x = 7$, and Bataceae have $n = 9$.

IV. *Dilleniidae*.—Here, again, $x = 7$ is rather clearly the original basic chromosome number, with aneuploidy and tetraploidy early events. Capparales appear to have had a tetraploid origin, with $x = 14$ and descending aneuploidy, as do Ebenales (ancestor may have had $x = 12$) and Primulales ($x = 12?$). The orders Ericales and Diapensiales have $x = 6$, suggesting an alternate hypothesis for the origin of Ebenales and Primulales. Cytological evidence seems not to favor Thorne's (1968) removal of Diapensiales to the Rosales, although there is other evidence for such a disposition. Salicales have $x = 19$ ($12 + 7$), and are therefore of paleohexaploid origin. Paeoniaceae have $x = 5$.

V. *Rosidae*.—Possibly $x = 7$, but with many early and important evolutionary changes. In Rosales, both Rosaceae and Crassulaceae have $x = 9$, and are possibly derived from a common ancestor with this chromosome number. Myrtales have apparently the unusual basic chromosome number of $x = 12$, whereas the probably related Cornales have $x = 11$. Rhizophoraceae ($x = 18, 32$) seem discordant in both groups, as do Thymelaeaceae, with $x = 9$. For Santalales, $x = 6$, which might also suggest the original basic chromosome number of the closely related Celastrales and Rhamnales, in which otherwise a tetraploid origin with $x = 12$ is suggested. Linales, Polygalales, and Umbellales all seem to have $x = 6$. Rutaceae are unusual in Sapindales ($x = 7$) and in the subclass, with $x = 9$ probable.

VI. *Asteridae*.—The original basic chromosome number for most orders seems again to have been $x = 7$, with early tetraploidy and subsequent aneuploid reduction. Lamiales evidently have had a tetraploid origin, with $x = 14$. Plantaginales have $x = 6$, with Brunoniaceae $x = 9$, and Goodeniaceae $x = 8, 9$. Rubiales may have $x = 11$, Dipsacales and Asterales $x = 9$.

As may be seen from the preceding review, $x = 7$ in each subclass of this class except Caryophyllidae, in which $x = 9$ for the most part. Magnoliidae and

Hamamelididae have a high proportion of families that probably had a polyploid origin, the other four subclasses fewer. Reduced basic chromosome numbers of $x = 6$ are characteristic of Ericales and Diapensiales (Dilleniidae); of Santalales, Linales, Polygalales, and Umbellales (Rosidae); and of Plantaginales (Asteridae). In each of these groups, tetraploids are much more common than diploids. Basic chromosome numbers reduced still further, to $x = 5$, seem to be characteristic of only four families: Paeoniaceae, Frankeniaceae, Limnanthaceae, and Callitrichaceae. These families are unrelated.

Order of dicots that seem to have had a polyploid origin are Nymphaeales ($x = 12-14$, if the very distinct *Nelumbo*, $x = 8$, is excluded); Trochodendrales ($x = 19$), Eucommiales ($x = 17$), Urticales ($x = 14$), Leitneriales ($x = 16$), Juglandales ($x = 16$), and Myricales ($x = 16$) of the Hamamelididae; Lecythidales (poorly sampled; $x = 13, 16, 17, 18$) and Salicales ($x = 19$) of the Dilleniidae; and Lamiales ($x = 14$) of the Asteridae. Other orders which might have had a polyploid origin are Polygonales ($x = 12, 11$, or 10), Capparales ($x = 12, 11$, or 10), Primulales ($x = 12$), Myrtales ($x = 12$), Celastrales ($x = 12$), and Cornales ($x = 11$). Additional information will probably clarify the situation in many of these groups.

It has long been realized that some families and subdivisions of families were of polyploid origin. More than 40 years ago, Karl Sax (1931, 1933) demonstrated that the subfamily Pomoideae of Rosaceae, with $x = 17$, was a paleopolyploid based upon $x = 9$, the original basic chromosome number for Rosaceae, and $x = 8$. Comparable subfamilial groups of paleopolyploid origin include Oleaceae—Oleoideae, $x = 23$ (Taylor, 1945); Bromeliaceae except for *Cryptanthus*, $x = 25$ (Marchant, 1967); Fabaceae—Mimosoideae, $x = 14$; most Bignoniaceae, $x = 20$; and a series of genera related to *Campanula* (Campanulaceae), $x = 17$. That polyploidy should be frequent in the origin of such groups, and of families, should not be surprising; Grant (1963: 486) has estimated that some 47% of the species of angiosperms are of polyploid origin.

Among the Magnoliales, all of the families have been sampled cytologically. Three of these have ambiguous basic chromosome numbers ($x = 10, 11$). Of the remaining 20, only two—Annonaceae and Trimeniaceae—had a diploid origin. Nine are evidently paleotetraploid, nine others, paleohexaploids. The most frequent chromosome number in Winteraceae, $n = 43$, is evidently paleododecaploid. Of the remaining 15 families of the subclass Magnoliidae for which information is available, seven have diploid basic numbers, seven polyploid numbers, and one (Saururaceae, $x = 11, 12?$) is ambiguous.

In Hamamelididae, the only diploids are found in Betulaceae-Carpinoideae, with $x = 8$, and in Casuarinaceae, with $x = 8, 9$. Of the remaining 14 families for which information is available, 10 have evidently had a tetraploid origin, four a hexaploid origin. Urticales have evidently been derived from a common tetraploid ancestor with $n = 14$.

In Caryophyllidae, 12 of the 13 families for which sufficient information is available seem to have been derived from diploid ancestors, with Basellaceae and Caryophyllaceae doubtful in this respect. The two chromosome counts reported for Didiereaceae range from $n = 75-100$.

For most of the remaining orders, the interpretation of many of the inferred basic chromosome numbers becomes ambiguous. In a particularly frequent situation, it is difficult to determine whether a group has had $x = 7$ followed by increasing aneuploidy, or tetraploidy on this number followed by decreasing aneuploidy. Only detailed knowledge of the orders and a careful evaluation of whether their constitution is appropriate will lead to the resolution of this question. Certain groups, on the basis of present knowledge, appear to have had particularly high basic chromosome numbers: among these, in addition to Didiereaceae, might be mentioned Actinidiaceae ($x = 29, 30$); Bombacaceae ($x = 36$ and higher numbers, with doubtful reports of $n = 14$ and 28 in *Durio*); Nepenthaceae ($x = 39$); and Pandanaceae ($x = 30$). Hippocastanaceae ($x = 20$), Platanaceae ($x = 21$), Salicaceae ($x = 19$), and many other families are presumably of paleohexaploid origin. An especially interesting pattern is found in families such as Araceae, Bignoniaceae, Bromeliaceae, and Oleaceae, in which paleotetraploids and paleohexaploids, but no diploids, are known to exist at present.

Families with basic chromosome numbers of $x = 9$ are fairly unusual, and include, in addition to most of those of the subclass Caryophyllidae, Thymelaeaceae and Rutaceae (Rosidae, certainly unrelated); and Brunoniaceae and perhaps Goodeniaceae (x might = 8), as well as the families of Dipsacales and Asterales of the Asteridae.

The discussion to this point demonstrates the limited utility of chromosome numbers in question of the placement of particular families. With the basic number $x = 7$ running throughout the dicots, and $x = 11-14$ especially frequent derivatives, only the most unusual chromosome number will tend either to confirm or deny a particular suggestion of affinity. On the other hand, chromosome numbers and morphology have been enormously useful within families and between closely related families in suggesting relationships. In addition, more conclusive information is required concerning the original basic chromosome number of many families. A few examples will illustrate the point; others have been mentioned in the detailed review above.

For example, Fouquieriaceae ($x = 12$) are placed by Hutchinson (1959) and by Cronquist (1968) in Violales and by Takhtajan (1969) in an order segregated from this alliance, Tamaricales; but Thorne (1968), on the basis of a detailed anatomical and morphological study, placed it in Solanales. Both Solanaceae and Tamaricaceae, families that have not been thought to be directly related, have $x = 12$. Takhtajan (1969) places Loasaceae ($x = 7$) in Polemoniales, Thorne (1968) and Cronquist (1968) places it in Violales (Cistales); both orders have $x = 7$. The examples could be multiplied. On the other hand, there are examples in which cytological evidence is more helpful.

The heterogeneity of Amentiferae is accepted by a majority of contemporary students of angiosperm phylogeny. It would be expected, therefore, that chromosomal evidence might be important in corroborating this heterogeneity. A summary of the basic chromosome numbers in this group, as recognized by Melchior (1964), is presented in Table 2.

Several points can be made concerning these families from the standpoint of cytology. Melchior's (1964) grouping of Myricales and Juglandales into a single

TABLE 2. Basic chromosome numbers in Archichlamydeae, orders 1-14 (Melchior, 1964).

Taxon	$x =$	Taxon	$x =$
1. Casuarinales		9. Santalales	
Casuarinaceae	8, 9	9a. Santalineae	
2. Juglandales		Olacaceae	10, 12, 19
Myricaceae	16	Dipentodontaceae	—
Juglandaceae	16	Opiliaceae	10
3. Balanopales		Grubbiaceae	—
Balanopaceae	—	Santalaceae	6, 5
4. Leitneriales		Myzodendraceae	—
Leitneriaceae	16	9b. Loranthineae	
5. Salicales		Loranthaceae	
Salicaceae	19	Loranthoideae	12
6. Fagales		Viscoideae	14, 10-13
Betulaceae	7? (8, 14)	10. Balanophorales	
Fagaceae	13 (14?)	Balanophoraceae	18
7. Urticales		11. Medusandrades	
Rhoipteleaceae	—	Medusandraceae	—
Ulmaceae	14	12. Polygonales	
Eucommiaceae	17	Polygonaceae	10, 11, 12
Moraceae	14	13. Centrospermae	9
Urticaceae	14	14. Cactales	
8. Proteales		Cactaceae	11
Proteaceae	7		

order is supported cytologically, and so would the notion of a close relationship between Leitnerales and this group. Eucommiaceae do not fit well into Urticales on cytological grounds, and they are separated by Cronquist (1968) and as a suborder by Thorne (1968). Santalales and Balanophorales appear distinctive cytologically. Polygonaceae appear distinct from Centrospermae, but then so do Cactaceae, linked with them by the presence of betalins. Garryaceae, once placed with Amentiferae, have $x = 11$ like other Cornales, and are now referred to that order.

What this review of chromosome numbers in Amentiferae perhaps illustrates, however, is that cytology provides no compelling reasons for separating these families or for grouping them. The relationships of Casuarinaceae are obscure and are not clarified by a consideration of the distinctive base chromosome numbers, $x = 8$ and 9 , in this group. They, together with Juglandales, Balanopales, Leitnerales, Fagales, and Urticales, are grouped by Cronquist (1968) in the subclass Hamamelididae, whereas only Casuarinales, Fagales, and Balanopales are included by Thorne (1968) in his superorder Hamamelidiflorae. Thorne allies Urticales with Malvales and other groups in his superorder Malviiflorae, but since Urticales, Malvales, Fagales, and the angiosperms as a whole all ultimately have a basic chromosome number of $x = 7$, no additional help is provided by cytology in making this decision. Salicales would have a distinctive basic chromosome number, $x = 19$, whether placed in Dilleniidae (Cronquist, 1968), Cistiflorae (Thorne, 1968), or left near Fagales (Melchior, 1964); however, the position accorded Salicaceae by Thorne and Cronquist does not differ in essence and

probably reflects the known facts better than the treatment of Melchior. Both Thorne (1968) and Cronquist (1968) regard Centrospermae (with Cactales and Polygonales) as an early evolutionary offshoot among the angiosperms, and their positions do not therefore differ much from that of Melchior (1964). Santalales and Balanophorales are regarded by both Thorne (1968) and Cronquist (1968) as related to Celastrales, and basic chromosome numbers of $x = 6$ and $x = 12$ are common to these groups. Whether Oleales are also related to this assemblage, as postulated by Thorne (1968), or to Asteridae (Cronquist, 1968), is open to question. Cytological evidence suggests that Celastrales, Santalales, and Rhamnales are related and derived from a common ancestor in which $x = 6$ relatively early in the history of the angiosperms; it does not support the placement of Oleaceae, with a basic chromosome number of $x = 14$ and probably ultimately $x = 7$, in a position of direct relationship to this group.

In his subclass Dilleniidae, Cronquist (1968) includes Thorne's (1968) superorder Cistiflorae in addition to his Theiflorae. Cytological evidence is inconclusive on this point; the groups are not highly distinctive and are regarded as related in both systems. Thorne's (1968) Malviiflorae includes, in addition to Urticales and Malvales, Euphorbiales, Solanales, Campanulales, and Rhamnales, all with basic chromosome numbers easily derived from $x = 7$. His superorder Santaliflorae, however, as already mentioned, includes only Santalales and Oleales. Rhamnaceae seem on cytological grounds to be allied to Celastrales, but Elaeagnaceae, allied by Thorne with Rhamnaceae, may have $x = 7$ ultimately instead of $x = 12$, and are probably better placed elsewhere. Cronquist (1968) and Takhtajan (1969) have placed them near Proteaceae, which also have $x = 7$. Oleales, also included by Thorne (1968) and Takhtajan (1969, as Celastranae) with Santaliflorae, also have $x = 7$, and are perhaps better included with Scrophulariales (Thorne's Bignoniales), following Cronquist (1968). In other words, cytological evidence suggests a modification of Thorne's Santaliflorae by the exclusion of Oleales and the addition of Rhamnaceae, Leeaceae, and Vitaceae, the latter two families assigned by Thorne (1968) to the Cornales, where they are cytologically discordant. Thorne's (1968) Santaliflorae would then be equivalent to Takhtajan's (1969) Celestranae, Takhtajan also including Oleales.

In Thorne's superorder Rutiflorae are included Rutales, Myricales, and Leitneriales. Juglandaceae (with Rhoipteleaceae) are placed in Rutales. Although the morphological and anatomical evidence for a relationship between Juglandaceae and such rutalean families as Anacardiaceae seems conclusive, cytological evidence also favors a common ancestry for the traditionally allied Juglandaceae, Myricaceae, and Leitneriaceae, all with $x = 16$. Perhaps these families, with Rhoipteleaceae, would better be treated as a second order of Rutiflorae. Cytologically they are discordant in Hamamelididae (unless directly related to *Liquidambar*), where placed by Cronquist (1968) and Takhtajan (1969), but fit very well with Rutales (Cronquist's Sapindales), where basic chromosome numbers of $x = 16$ are frequent. In Cronquist's system, they should probably constitute an order or orders following Sapindales. As stressed by Takhtajan (1969: 104-105), the very reduced flowers of plants such as *Leitneria* make their affinities very difficult to determine.

Thorne's (1968) superorder Gentianiflorae includes Bignoniales (Scrophulariales), $x = 7$, and Gentianales, with the same composition as Cronquist's group together with Rubiaceae (essentially the arrangement of Melchior, 1964). The basic chromosome number for Gentianales may be $n = 7$, but Apocynaceae and Asclepiadaceae, as well as .Antoniaceae and Strychnaceae (segregates from Loganiaceae), have $x = 11$ like Rubiaceae. Cronquist's (1968) placement of Rubiaceae as a unifamilial order near Campanulales and Dipsacales is neither favored nor strongly contradicted by cytological evidence, but Thorne's treatment resembles that of Takhtajan (1969) and is perhaps more conservative.

On cytological grounds, there seems to be a relationship between a number of orders of Cronquist's (1968) Rosidae: Linales, Polygalales, and Umbellales, with $x = 6$, Myrtales perhaps with $x = 12$, Cornales with $x = 11$, and perhaps even Santalales ($x = 6$), Celastrales ($x = 12$), and Rhamnales ($x = 12$). The special relationship between Cornales and Umbellales in Cronquist's sense, implied by Thorne's grouping them into an order Cornales, is uncertain, and there seems to be some relationship between Myrtales and this group.

Cytological evidence, like the evidence from floral anatomy (Eyde, this symposium), tends to contradict a derivation of Proteaceae ($x = 7$) and Elaeagnaceae ($x = 7$) from Myrtales ($x = 12, 11$), where Thymelaeaceae ($x = 9$) are also apparently discordant. All three families might be accommodated more easily earlier in the rosid line.

These and other questions must, however, be decided in the light of all the evidence, and what is feasible cytologically might be contradicted on other grounds. Nevertheless, cytology does have its contribution to make to our understanding the bases of angiosperm phylogeny. We are now able to improve on the pioneering efforts of Darlington & Mather (1949), especially in view of the fact that information is available for three times as many genera—perhaps 40% of the total. When more of the gaps have been filled, and especially when we have the results of comprehensive investigations of many families in which chromosomal evidence is combined with all other available evidence to produce a reasonable hypothesis concerning original basic chromosome number, it will be possible to advance our deductions about the patterns of cytological evolution in the angiosperms still farther.

THE PATTERN IN LILIOPSIDA (MONOCOTYLEDONEAE)

As should be evident from the summary presented earlier, much less can be said about the evolution of chromosome numbers in monocots than in dicots. Certainly $x = 7$, the original basic chromosome number of angiosperms, is much in evidence in the monocots as well as in the dicots, and could easily be the original basic chromosome number for Alismatales, Hydrocharitales ($x = 6$ is also frequent), Restionales, Zingiberales, and Arales on the basis of present evidence. For the large families Commelinaceae, Liliaceae sensu lato, and Orchidaceae, although there is much information about chromosomes, it would clearly be premature to advance a hypothesis concerning the original basic number. High basic chromosome numbers are characteristic of Flagellariaceae, $x = 19$; Bromeliaceae, $x = 17, 25$; Arecaceae, $x = 18$; and Pandanaceae, $x = 30-32$. The

first three of these are at least paleotraploid, the last at least paleohexaploid. The systems for the monocots of Hutchinson (1959), Melchior (1964), Thorne (1968), Cronquist (1968), and Takhtajan (1969) are similar enough that there are relatively few problems of placement to discuss in the light of cytological evidence. The vexed subject of family limits in the Liliales is one in which cytological information is not helpful, although there is a great cytological diversity which will continue to be helpful in understanding the relationships of particular species and genera.

EVOLUTIONARY TRENDS

Even though evolutionary changes in chromosome number and morphology have been frequent and may seem to have given rise to a bewildering diversity of situations (Stebbins, 1971), some generalities can be derived concerning evolutionary trends. Among them are the following.

The original basic chromosome number in angiosperms seems clearly to have been $x = 7$, characteristic of all major groups of both dicots and monocots except Caryophyllidae, with $x = 9$. This implies clearly that most progressive evolution has been at the diploid level (Stebbins, 1950, 1967, 1970), even though polyploidy has been very important in the evolution of families and even orders. The subclasses devised by Armen Takhtajan more than a decade ago have remained very useful conceptually, but the distinctions between Dilleniidae and Rosidae seem to be more and more dubious (Eyde, this symposium), and Asteridae may be diphyletic (Hickey & Wolfe, this symposium). When these lines are better understood, so will be the pattern of chromosomal evolution they have undergone.

It is of interest to compare the original basic chromosome number of angiosperms with those found in various groups of gymnosperms. *Ephedra* has $x = 7$ and *Welwitschia*, $x = 21$, but there are a variety of reasons for doubting that they had a common ancestor with angiosperms in which $n = 7$. *Gnetum* has $x = 12$. In the Coniferophyta, *Ginkgo* has $n = 12$, as do a variety of other genera, with $n = 11$ also very frequent. Noteworthy are Araucariaceae and *Pseudotsuga* (Pinaceae) with $n = 13$, *Sciadopitys* (Taxodiaceae) with $n = 10$, and a great variety of chromosome numbers in Podocarpaceae. In Cycadophyta, $n = 8, 9$, and 11 are represented (Marchant, 1968).

The high incidence of polyploidy in Annoniflorae and Hamamelidiflorae strongly suggests that the ancestors of many of the surviving families were polyploids that invaded newly opened habitats in mid-Cretaceous time (Stebbins, 1950). The opening of these habitats and the success of the early angiosperms might well be correlated with climatic changes accompanying the opening of the Indian Ocean 150 million years ago, and especially with the separation of Africa from South America which began 125–130 million years ago (summary in Raven & Axelrod, 1974). On the other hand, polyploids are not so well represented among the basal orders of Cronquist's Dilleniidae, including families such as Dipterocarpaceae which are typical of the tropical lowland rain forest. As stressed by Takhtajan (1969), many of the primitive members of Annoniflorae and Hamamelidiflorae occur in subtropical mountains with a very equitable climate, and not in the tropical lowland forest. This suggests that the "newly opened

habitats" mentioned above may not have been the tropical lowland forest, but rather the relatively temperate mountains in or near the tropics. An expansion of such habitats is not known to have occurred in the mid-Cretaceous. It may be that polyploids have simply accumulated in the equitable tropical mountains and islands as conservative offshoots of the mainstream of angiosperm evolution, with polyploidy itself playing a retarding role on progressive evolution.

LITERATURE CITED

- AIRY SHAW, H. K. 1966. J. C. Willis. A Dictionary of the Flowering Plants and Ferns. Ed. 7. Cambridge Univ. Press, Cambridge. xxii + 1214 + liii pp.
- BAKER, H. G. & I. BAKER. 1968. Chromosome numbers in the Bombacaceae. Bot. Gaz. (Crawfordsville) 129: 294-296.
- BARLOW, B. A. 1959. Chromosome numbers in the Casuarinaceae. Austral. Jour. Bot. 7: 231-237.
- & D. WIENS. 1971. The cytogeography of the loranthaceous mistletoes. Taxon 20: 291-312.
- BATES, D. M. & O. J. BLANCHARD, JR. 1970. Chromosome numbers in the Malvales. II. New or otherwise noteworthy counts relevant to classification in the Malvaceae, tribe Malveae. Amer. Jour. Bot. 57: 927-934.
- BAWA, K. 1973. Chromosome numbers of tree species of a lowland tropical community. Jour. Arnold Arbor. 54: 422-434.
- BECKER, K. M. 1973. A comparison of angiosperm classification systems. Taxon 22: 19-50.
- BENNETT, E. M. 1972. A revision of the Australian species of *Hybanthus* Jacquin (Violaceae). Nuytsia 1: 218-241.
- BEUSEKOM-OSINGA, R. J. VAN & C. F. VAN BEUSEKOM. 1975. Delimitation and subdivision of the Crypteroniaceae (Myrtales). Blumea 22: 255-266.
- BLAKE, S. T. 1972. *Idiospermum* (Idiospermaceae), a new genus and family for *Calycanthus australiensis*. Contr. Queensland Herb. 12: 1-38.
- BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA & O. ZAKHARYEVA. 1969. Chromosome Numbers of Flowering Plants. V. L. Komarov Botanical Inst., Academy of Sciences of the U.S.S.R. 926 pp.
- BRIGGS, B. G. 1963. Chromosome numbers in *Lepyrodia* and *Restio* in Australia. Contr. New South Wales Natl. Herb. 3: 228-232.
- . 1966. Chromosome numbers of some Australian monocotyledons. Contr. New South Wales Natl. Herb. 4: 24-34.
- . 1970. Some chromosome numbers in the Oleaceae. Contr. New South Wales Natl. Herb. 4: 126-129.
- BRIQUET, J. 1895. Labiatae. In A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien. IV, 3a: 183-380. Wilhelm Engelmann, Leipzig.
- BROWN, W. V. & B. N. SMITH. 1972. Grass evolution, the Kranz syndrome, $^{13}\text{C}/^{12}\text{C}$ ratios, and continental drift. Nature 239: 345-346.
- BURTT, B. L. 1962. Studies on the Gesneriaceae of the Old World. XXIV. Tentative keys to the tribes and genera. Notes Roy. Bot. Gard. Edinburgh 24: 205-220.
- CAROLIN, R. C. 1960. The structures involved in the presentation of pollen to visiting insects in the order Campanulales. Proc. Linn. Soc. New South Wales 85: 166-177.
- CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin Co., Boston. xi + 396 pp.
- DARLINGTON, C. D. 1956. Chromosome Botany. George Allen & Unwin, Ltd., London. xii + 186 pp.
- & E. K. JANAKI AMMAL. 1945. Chromosome Atlas of Cultivated Plants. George Allen & Unwin, Ltd., London. 397 pp.
- & K. MATHER. 1949. The Elements of Genetics. George Allen & Unwin, Ltd., London.
- & A. P. WYLIE. 1955. Chromosome Atlas of Flowering Plants. George Allen & Unwin, Ltd., London. xix + 519 pp.
- DARMER, G. 1947. Rassenbildung bei *Hippophaë rhamnoides* (Sanddorn). Biol. Zentralbl. 66: 166-170.
- DING HOU. 1972. Germination, seedling, and chromosome number of *Scyphostegia borneensis* Stapf (Scyphostegiaceae). Blumea 20: 88-92.

- EHRENDORFER, F. 1964. Evolution and karyotype differentiation in a family of flowering plants: Dipsacaceae. *Genetics Today*. Pp. 399–407. Pergamon Press, Oxford.
- . in press. Evolutionary significance of chromosomal differentiation patterns in gymnosperms and primitive angiosperms. In C. B. Beck (editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York.
- , F. KRENDL, E. HABELER & W. SAUER. 1968. Chromosome numbers and evolution in primitive angiosperms. *Taxon* 17: 337–353.
- ERNST, W. R. 1962. The genera of Papaveraceae and Fumariaceae in the southeastern United States. *Jour. Arnold Arbor.* 43: 315–343.
- EYDE, R. H. 1966. Systematic anatomy of the flower and fruit in *Corokia*. *Amer. Jour. Bot.* 53: 833–847.
- FRIERSON, J. L. 1959. Cytotaxonomic study of selected indigenous and introduced species of the genus *Ilex* commonly grown in the United States. Ph.D. dissertation, Univ. of South Carolina. 76 pp.
- GADELLA, T. W. J. 1972. Cytological studies on some flowering plants collected in Africa. *Bull. Jard. Bot. Natl. Belgique* 42: 393–402.
- GOLDBLATT, P. 1971. Cytological and morphological studies in the southern African Iridaceae. *Jour. S. African Bot.* 37: 317–460.
- . 1974. A contribution to the knowledge of cytology in Magnoliales. *Jour. Arnold Arbor.* 55: 453–457.
- . 1976a. New or noteworthy chromosome records in the angiosperms. *Ann. Missouri Bot. Gard.* 63: in press.
- . 1976b. Chromosome cytology in the Bruniaceae. *Jour. S. African Bot.*: in press.
- . 1976c. Cytotaxonomic studies in the tribe Quillajeae (Rosaceae). *Ann. Missouri Bot. Gard.* 63: in press.
- & R. KEATING. 1976. Chromosome number and pollen structure in *Retzia capensis* Thunb. *Ann. Missouri Bot. Gard.* 63: in press.
- GRANT, V. 1959. *Natural History of the Phlox Family*. Vol. 1. Systematic Botany. Martinus Nijhoff, The Hague. xiv + 280 pp.
- . 1963. *The Origin of Adaptations*. Columbia Univ. Press, New York. x + 606 pp.
- GRANT, W. F. 1955. A cytogenetic study in the Acanthaceae. *Brittonia* 8: 121–149.
- GREGORY, W. C. 1941. Phylogenetic and cytological studies in the Ranunculaceae Juss. *Trans. Amer. Philos. Soc.* 31: 443–520.
- HANS, A. S. 1973. Chromosomal conspectus of the Euphorbiaceae. *Taxon* 22: 591–636.
- HARRIS, B. D. 1968. Chromosome numbers and evolution in North American species of *Linum*. *Amer. Jour. Bot.* 55: 1197–1204.
- HUBER, H. 1969. Die Samenmerkmale und Verwandtschaftsverhältnisse der Liliifloren. *Mitt. Bot. Staatssamml. München* 8: 219–538.
- HUTCHINSON, J. 1959. *The Families of Flowering Plants. Dicotyledons*. 2 vols. Clarendon Press, Oxford. x + 1–510 pp; x + 511–792 pp.
- JEFFREY, C. 1962. Notes on Cucurbitaceae, including a proposed new classification for the family. *Kew Bull.* 15: 337–371.
- JOHNSON, L. A. S. 1957. A review of the family Oleaceae. *Contr. New South Wales Natl. Herb.* 2: 395–418.
- & B. G. BRIGGS. 1963. Evolution in the Proteaceae. *Austral. Jour. Bot.* 11: 21–61.
- JONES, K. 1967. The chromosomes of orchids: II. Vandeae Lindl. *Kew Bull.* 21: 151–156.
- & C. JOPLING. 1972. Chromosomes and the classification of the Commelinaceae. *Bot. Jour. Linn. Soc.* 65: 129–162.
- & J. B. SMITH. 1966. The cytogeography of *Impatiens* L. (Balsaminaceae). *Kew Bull.* 20: 63–72.
- KRAPOVICKAS, A. 1972. La información cromosómica y su importancia en la sistemática. *Mem. Symp. I Congr. Latinoamer. Bot.*, pp. 247–264. Sociedad Botánica México, S. A.
- KRUPKO, S. 1962. Embryological and cytological investigations in *Hypodiscus aristatus*. *Jour. S. African Bot.* 28: 21–44.
- KUNDU, B. C. & A. DE. 1968. Taxonomic position of the genus *Nyctanthes*. *Bull. Bot. Surv. India* 10: 397–408.
- KURABAYASHI, M., H. LEWIS & P. H. RAVEN. 1962. A comparative study of mitosis in the Onagraceae. *Amer. Jour. Bot.* 49: 1003–1026.
- LEWIS, H. 1960. Chromosome numbers and phylogeny of *Trichostema*. *Brittonia* 12: 93–97.
- LÖVE, A. & D. LÖVE. 1961. Chromosome numbers of central and northwest European plant species. *Opera Bot.* 5: 1–581.

- MAHANTY, H. K. 1970. A cytological study of the Zingiberales with special reference to their taxonomy. *Cytologia* 35: 13-49.
- MARCHANT, C. J. 1967. Chromosome evolution in the Bromeliaceae. *Kew Bull.* 21: 161-168.
- . 1968. Chromosome patterns and nuclear phenomena in the cycad families *Strangeriaceae* and *Zamiaceae*. *Chromosoma* 24: 100-134.
- MATHIAS, M. E. & L. CONSTANCE. 1955. The genus *Oreomyrrhis* (Umbelliferae). A problem in South Pacific distribution. *Univ. Calif. Publ. Bot.* 27: 347-416.
- McKELVEY, S. D. & K. SAX. 1933. Taxonomic and cytological relationships of *Yucca* and *Agave*. *Jour. Arnold Arbor.* 14: 76-81.
- MEHRA, P. N. & B. S. GILL. 1971. Further observations on B-chromosomes in Himalayan hardwoods. *Jour. Indian Bot. Soc.* 50A: 377-380.
- & P. K. KHOSLA. 1969. In IOPB chromosome number reports: 20. *Taxon* 18: 215-220.
- & ———. 1972. Cytogenetical studies of East Himalayan Hamamelidaceae, Combretaceae and Myrtaceae. *Silv. Genet.* 21: 186-190.
- , T. S. SAREEN & P. K. KHOSLA. 1972. Cytological studies on Himalayan Meliaceae. *Jour. Arnold Arbor.* 53: 558-568.
- MEIJER, W. 1972. The genus *Axinandra*—Melastomataceae: a missing link in Myrtales? *Ceylon Jour. Sci.* 10: 72-74, pl. 1.
- MELCHIOR, H. (editor). 1964. A. Engler's Syllabus der Pflanzenfamilien. Ed. 12. Vol. 2. Angiospermen. Gebrüder Borntraeger, Berlin. 666 pp.
- MOORE, H. E., JR. & R. E. LEE. 1967. The broadening basis of classification in the Gesneriaceae. *Baileya* 15: 97-108.
- & N. W. UHL. 1973. Palms and the origin and evolution of monocotyledons. *Quart. Rev. Biol.* 48: 414-436.
- MOORE, R. J. (editor). 1974. Index to plant chromosome numbers: 1972. *Regnum Veg.* 91: 1-108.
- NANDA, P. C. 1962. Chromosome number of some trees and shrubs. *Jour. Indian Bot. Soc.* 41: 271-277.
- NEVLING, L. I., JR. 1969. The ecology of an elfin forest in Puerto Rico, 5. Chromosome numbers of some flowering plants. *Jour. Arnold Arbor.* 50: 99-103.
- PEACOCK, W. J. 1963. Chromosome numbers and cytoevolution in the Goodeniaceae. *Proc. Linn. Soc. New South Wales* 88: 8-27.
- PERDUE, R. E., JR., R. L. SMITH, M. E. WALL, J. L. HARTWELL & B. J. ABBOTT. 1970. *Camptotheca acuminata* Decaisne (Nyssaceae), source of camptothecin, an antileukemic alkaloid. *Tech. Bull. U.S.D.A.* 1414: 1-26.
- RATTER, J. A. 1975. A survey of chromosome numbers in the Gesneriaceae of the Old World. *Notes Roy. Bot. Gard. Edinburgh* 33: 527-543.
- & C. MILNE. 1973. Chromosome numbers of some primitive angiosperms. *Notes Roy. Bot. Gard. Edinburgh* 32: 423-428.
- RAVEN, P. H. & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539-673.
- & M. S. CAVE. 1963. Chromosome numbers in *Crossosoma*. *Madroño* 17: 68.
- & D. W. KYHOS. 1961. Chromosome numbers in Compositae II. Helenieae. *Amer. Jour. Bot.* 48: 842-850.
- & ———. 1965. New evidence concerning the original basic chromosome number of angiosperms. *Evolution* 19: 244-248.
- , ——— & M. S. CAVE. 1971. Chromosome numbers and relationships in Annoniflorae. *Taxon* 20: 479-483.
- , O. T. SOLBRIG, D. W. KYHOS & R. SNOW. 1960. Chromosome numbers in Compositae. I. Astereae. *Amer. Jour. Bot.* 47: 124-132.
- ROBSON, N. K. B. & P. ADAMS. 1968. Chromosome numbers in *Hypericum* and related genera. *Brittonia* 20: 95-106.
- ROLLINS, R. C. 1969. A remarkable new crucifer from Mexico. *Contr. Gray Herb.* 198: 3-8.
- ROUSI, A. 1965. Observations on the cytology and variation of European and Asiatic populations of *Hippophaë rhamnoides*. *Ann. Bot. Fenn.* 2: 1-18.
- . 1971. The genus *Hippophaë* L. A taxonomic study. *Ann. Bot. Fenn.* 8: 177-227.
- RÜDENBERG, L. 1967. The chromosomes of *Austrobaileya*. *Jour. Arnold Arbor.* 48: 241-244.
- SANTAMOUR, F. S., JR. 1972. Chromosome numbers in *Liquidambar*. *Rhodora* 74: 287-290.
- SAX, K. 1931. The origin and relationships of the Pomoideae. *Jour. Arnold Arbor.* 12: 2-22.
- . 1933. The origin of the Pomoideae. *Proc. Amer. Soc. Hort. Sci.* 30: 147-150.

- SENN, H. A. 1938. Chromosome number relationships in the Leguminosae. *Bibliogr. Genet.* 12: 175-336.
- SHARMA, A. K. & I. GHOSH. 1971. Cytotaxonomy of the family Bromeliaceae. *Cytologia* 36: 237-247.
- SIMMONDS, N. W. 1962. *The Evolution of the Bananas*. Longmans, Green and Co., Ltd., London. xii + 170 pp.
- SMITH, A. C. 1972. An appraisal of the orders and families of primitive extant angiosperms. *Jour. Indian Bot. Soc.* 50A: 215-226.
- SMITH, J. B. 1966. Chromosome numbers in *Peperomia* Ruiz & Pav. (Piperaceae) and a note on the chromosome number of *Piper magnificum* Trelease. *Kew Bull.* 20: 521-526.
- SMITH-WHITE, S. 1959. Cytological evolution in the Australian flora. *Cold Spring Harbor Symp. Quant. Biol.* 24: 273-289.
- SOEPADMO, E. 1972. Fagaceae. *In* *Flora Malesiana*, Ser. I, 7: 265-403.
- SOLBRIG, O. T., L. C. ANDERSON, D. W. KYHOS, P. H. RAVEN & L. RÜDENBERG. 1964. Chromosome numbers in Compositae. V. Astereae II. *Amer. Jour. Bot.* 51: 513-519.
- STEBBINS, G. L. 1950. *Variation and Evolution in Plants*. Columbia Univ. Press, New York. xx + 643 pp.
- . 1966. Chromosomal variation and evolution. *Science* 152: 1363-1439.
- . 1967. Adaptive radiation and trends of evolution in higher plants. *In* T. Dobzhansky, M. K. Hecht & W. C. Steere (editors), *Evolutionary Biology*. Vol. 1: 101-142. Appleton-Century Crofts, New York.
- . 1970. Adaptive radiation of reproductive characteristic in angiosperms, I: Pollination mechanisms. *Annual Rev. Ecol. Syst.* 1: 307-326.
- . 1971. *Chromosomal Evolution in Higher Plants*. Addison-Wesley Publ. Co., Reading, Massachusetts viii + 216 pp.
- , J. A. JENKINS & M. S. WALTERS. 1953. Chromosomes and phylogeny in the Compositae, tribe Cichorieae. *Univ. Calif. Publ. Bot.* 26: 401-429.
- STYLES, B. T. & C. G. VOSA. 1971. Chromosome numbers in the Meliaceae. *Taxon* 20: 485-499.
- SUGIURA, T. 1936. Studies on the chromosome numbers of higher plants, with special reference to cytokinesis, I. *Cytologia* 7: 544-595.
- SWAMY, B. G. L. 1953. The morphology and relationships of the Chloranthaceae. *Jour. Arnold Arbor.* 34: 375-408.
- TAKHTAJAN, A. 1969. *Flowering Plants: Origin and Dispersal*. Transl. by C. Jeffrey. Smithsonian Inst. Press, Washington, D. C. x + 310 pp.
- TAYLOR, H. 1945. Cyto-taxonomy and phylogeny of the Oleaceae. *Brittonia* 5: 337-367.
- THORNE, R. F. 1963. Some problems and guiding principles of angiosperm phylogeny. *Amer. Naturalist* 97: 287-305.
- . 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* 6: 57-66.
- . 1973. Inclusion of the Apiaceae (Umbelliferae) in the Araliaceae. *Notes Roy. Bot. Gard. Edinburgh* 32: 161-165.
- . 1974. A phylogenetic classification of the Annoniflorae. *Aliso* 8: 147-209.
- TURNER, B. L. & O. S. FEARING. 1959. Chromosome numbers in the Leguminosae II: African species, including phyletic interpretations. *Amer. Jour. Bot.* 46: 49-57.
- TUTAJUK, V. X. & L. V. TURCHANINOVA. 1970. The chromosome number of the chestnut-leaf oak, *Quercus castaneifolia* C. A. M. *Dokl. Akad. Nauk Azerbajdzansk. S.S.R.* 24: 47-50. [In Russian.]
- VERDCOURT, B. 1958. Remarks on the classification of the Rubiaceae. *Bull. Jard. Bot. État* 28: 209-290.
- WALKER, J. W. 1971. Pollen morphology, phytogeography, and phylogeny of the Annonaceae. *Contr. Gray Herb.* 202: 1-132.
- . 1972. Chromosome numbers, phylogeny, phytogeography of the Annonaceae and their bearing on the (original) basic chromosome number of angiosperms. *Taxon* 21: 57-65.
- WEBSTER, G. L. 1967. The genera of Euphorbiaceae in the southeastern United States. *Jour. Arnold Arbor.* 48: 303-430.
- WHITAKER, T. W. 1933. Chromosome number and relationship in the Magnoliales. *Jour. Arnold Arbor.* 14: 376-385.
- WIENS, D. & B. A. BARLOW. 1971. The cytogeography and relationships of the viscaceous and eremolepidaceous mistletoes. *Taxon* 20: 313-332.



Raven, Peter H. 1975. "The Bases of Angiosperm Phylogeny: Cytology." *Annals of the Missouri Botanical Garden* 62, 724–764. <https://doi.org/10.2307/2395272>.

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