Chromosome Numbers in Gymnosperms

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The gymnosperms, though possessing fewer genera and species in comparison to the angiosperms, however, constitute a dominant element of the forests in the temperate zones of the earth. The group has not only considerable phylogenetic importance, but also constitutes very important source of wood (used for diverse purposes), resins, oleoresins, gums, essential oils, medicines and some edible starches and seeds (cf. Schery, 1954; Thieret, 1958 etc.). The more important component of the group, namely, the *Coniferales*, is now receiving considerable attention all over the world, at the hands of morphologists, palaeontologists and breeders. The importance of the cytological data in all such studies requires no emphasis. As such the need for a consolidated and an up-to-date list of chromosome numbers of the gymnosperms has been felt by the present writer and also pointed out repeatedly by several colleagues (in particular W. Langner, Schmalenbeck) interested in various aspects of this primitive but fascinating group of seed plants. During the course of the writer's association with the cytogenetical aspect of this group, he has gathered such data from different sources. This paper consolidates most of the scattered literature on the topic and helps us not only to take stock of the present achievements in this field, but, what is more important, it reveals to us as to what remains to be accomplished.

Eversince the publication of the classical cytological works of Karl Sax and his collaborators (1932—34), several papers on the cytology (sometimes also on the cytogenetics) of the Northern conifers (sensu Florin, 1940) have appeared. All these will be reviewed in a forthcoming publication of the writer. However, mention must be made of the recent valuable work by Hair and Beuzenberg (1958a, b) which has filled the long-felt gap in our knowledge of the cytological situation in the southern conifers, in particular the *Podocarpaceae*. This family is „taxonomically complex and morphologically very variable" (Mehra and Khoshoo, 1956b) and in agreement with this statement, the family has also turned out to be cytologically heterogeneous (cf Hair and Beuzenberg, 1958a, b). This heterogeneity is unparalleled in gymnosperms in particular, and tree species in general. These authors have studied 52 species covering all the 7 genera of the family *Podocarpaceae*. The haploid number ranges from 9 to 19. There is a „regular numerical relationship" between the number of metacentric and subtelocentric chromosomes. According to them the trend has been towards reduction in the number of chromosomes by the „fusion" of subtelocentrics. It must be admitted that their results are highly significant and a fuller version of their findings is awaited with considerable interest and anticipation.

Mention may also be made of the recent theoretical paper by the present writer (Khoshoo, 1958, 1959) in which he evaluated the role of polyploidy in gymnosperms in general, and conifers in particular. This is the first of the series of papers evaluating the role of various cytogenetic factors responsible for the evolution within the gymnosperms. He has shown that the present data reveal that polyploidy is totally absent in *Cycadales, Ginkgoales,* Welwitschiales and Gnetales. The *Coniferales* contain merely 1.5% and *Ephedrales* about 44.4% of polyploids (Khoshoo, 1958; 1959, Table 2). Each and every case of natural polyploidy (seedlings, trees, species and genera), in particular within *Coniferales*, has been critically evaluated and the nature of its polyploidy diagnosed on the various grounds. The causes of the rarity of polyploidy have been critically reviewed. The original hypothesis of Darlington (1937, p. 84) that in trees the nuclear-cytoplasmic ratio has already reached a perfect equilibrium and is at present at an „upper limit", that is at a stage when any alteration is deleterious, can be part of the explanation for the rarity af polyploidy in gymnosperms in general, and conifers in particular. The change in the equilibrium by polyploidy results in weak and slow-growing individuals which have no selective advantage, because in nature fast-growing individuals are favoured. Furthermore, the writer has for the first time brought out that so far all the cases of polyploid seedlings and trees have been only detected in protected habitats (nurseries and experimental farms) where competition is almost totally lacking and thus conditions are very favourable for the growth of such aberrant types.

In the opinion of the writer the other, and rather a more plausible, reason for the rarity of polyploidy is as follows. The present data reveal that there is an ecospecific differentiation between all the compatible taxa. As such polyploid resulting from hybrids involving even morphologically distinct species, will be largely auto- or segmental alloploid in nature. That such polyploids have been unable to establish and then to diverge into perfect alloploid is clear from the fact, that even though polyploid seedlings arise constantly in *Coniferales*, yet polyploidy is rare in this group (Khoshoo, 1958, pp. 24—31; 1959, pp. 32—34). Polyploids with such cytogenetic properties have very small chance of survival, particulary because of their being poor competitors and the absence of apomixis (vegetative reproduction and/or agamospermy). It is well known that apomixis lends a helping hand in averting the „bottleneck" of initial sterility in raw polyploids. Why agamospermy is rare in gymnosperms is an interesting question, and will be answered elsewhere.

Lastly the writer (Khoshoo, 1958, pp. 5—6; 1959, p. 26) has pointed out that polyploidy as a tool for raising improved conifers is likely to be generally unrewarding, because of the poor growth and fertility of the induced polyploids in this group. Perhaps the only hope is to raise auto- and allotriploids, which, as is known from the researches of the Swedish workers (Müntzing, 1936; Johnsson, 1945, 1950, 1953) are useful in some dicotyledonous trees. The triploid *Larix* raised after interspecific cross by Syrach Larsen and Westergaard (1938) is fairly vigorous and is, therefore, a pointer in this direction (cf. Khoshoo, 1958, pp. 5—6; 1959, p. 26). Such vigorous triploids could be multiplied further by vegetative means.

In another communication the writer (Khoshoo, 1960) evaluated the role of karyotypic changes in the evolution and differentiation of gymnosperms in general, and conifers in particular. It has been brought out that the various processes involved at various levels are translocations, fragmentation-fusion processes, segmental interchanges, periand paracentric inversions and cryptic structural hybridity. These have resulted in alterations in number and morphology, and repatterning of chromosomes without significant changes in the karyotype.

It has been concluded that in the gymnosperms the various organs (including the nucleus) seem to have advanced at different rates. As such it is not possible to form a rigid evolutionary series taking all characters into consideration. However, in general, cytological data follow the taxonomic groupings and in the various families (except *Cycadaceae* and *Podocarpaceae)* a single basic number can be recognised. In these two families the basic numbers in the present day genera form a dysploid series resulting from fragmentation and/or fusion of centromeres. Judging from our present day understanding of the karyotypic evolution in plants in general, it is tempting to speculate that the probable ancestral karyotype in these families was low-numbered and symmetrical.

The various genera in a family may or may not resemble one another in their basikaryotype which remains generally constant within genera except in *Podocarpus* and *Dacrydium.* However, in the later genera basikaryotype remains constant only in some sections. The inter- and intraspecific differentiation is due to changes in absolute size of the chromosome complement and/or number, nature and location of secondary constrictions and satellites. Furthermore, apart from gene mutations, such differentiation involves other changes like segmental interchanges, inversions and cryptic structural hybridity.

The decrease in chromosome number and absolute size of chromosomes of a complement seems to be generally correlated with the phylogenetic advancement in conifers. Similarly the increase in asymmetry can also be correlated in some cases with specialization in habitat, habit and morphology.

In comparison to angiosperms, the gymnosperms are cytogenetically extremely stable. Such stability is also found in their habitat preferences, habit, morphology and pollination, and reproductive systems etc.

In the end avenues for further work have been pointed out.

The above are among the notable works that have appeared in recent years on the topic. We may now proceed to make some explanatory remarks on the present paper.

Apart from the original papers, the following works have been consulted while preparing the present list:

Maude (1939), Darlington and Janaki Ammal (1945), Löve and Löve (1948), Kanezawa (1949), Satô (1949, pp. 162—169), Delay (1950—1951), Stiff (1952), Darlington and Wylie (1955), Cave et al (1956—1959 and supplement) and Khoshoo (1959).

Generally the data from older morphological works, which in most cases have either been doubtfully reported or have turned out to be incorrect after using improved techniques, have not been quoted. Only authentic reports of the natural polyploids have been included (Khoshoo, 1958, 1959). Cytological data on hybrids have also been included.

The arrangement of the families is adapted after Takhtajan (1953) and that of genera within families after Sax and Sax (1933) for *Cycadales* and after Li (1953) for *Coniferales.* The validity of the specific names in *Ephedra* has been checked from the Index Kewensis (1895—1950) and that of the *Coniferales* mostly from Dallimore and Jackson (1948). The species of conifers marked with an asterisk are not given in Dallimore and Jackson (1948) but are included in the Index Kewensis (1895—1950).

At present out of about 67 genera, 55 (82 %) genera and out of about 635 species, 264 (42%) species have been cytologically studied. After a perusal of all these data, the writer feels that work along the following lines is important and needs particular attention.

1. The following genera urgently need a cytological study, since no work has been done so far on them.

Taxaceae	: *Austrotaxus, Nothotaxus.*
Pinaceae	: *Cathaya* (cf. Chun and Kuang, 1958).
Taxodiaceae	: *Glyptostrobus.*
Cupressaceae	: *Fitzroya, Neocallitropsis, Octoclinis, Diselma, Papuacedrus, Pilgerodendron, Fokienia, Heyderia, Arceuthos.*

2. Cytogenetic studies are needed on interspecific and intergeneric hybrids. Such studies have been almost altogether neglected so far, even though very important and valuable work is being done on the breeding of conifers all over the world. The urgent need for such data has been already emphasised by the present writer (Khoshoo, 1958, 1959). Such studies would also go a long way to elucidate the cytogenetic basis of the species and the generic relationships. It is needless to mention here that some probable cases of intergeneric hybrids are already on record in the literature: *Ceratozamia* × *Zamia* (Chamberlain, 1926), four hybrids involving *Tsuga, Picea* and *Keteleeria* (Campo-Duplan and Gaussen, 1949) and *Cupressus* × *Chamaecyparis* (Osborn, 1940).

3. Critical cytogenetic work is needed on the polyploid trees and species and also on the polyploid seedlings often discovered in nurseries.

4. More work is needed to supplement the existing state of knowledge on the following genera:

Cycadaceae	: *Cycas, Macrozamia, Encephalartos, Zamia.*
Araucariaceae	: *Araucaria, Agathis.*
Taxaceae	: *Amentotaxus, Torreya.*
Pinaceae	: *Keteleeria, Abies, Pseudotsuga, Larix.*
Cupressaceae	: *Libocedrus, Juniperus.*
Ephedraceae	: *Ephedra.*
Welwitschiaceae	: *Welwitschia.*
Gnetaceae	: *Gnetum.*

There are several foresters and forest-tree breeders in the world to whom the viable seeds of the species of the above genera are easily available. I will feel deeply grateful to anyone sending me the viable seeds of these, in particular of the totally unworked genera listed earlier.

Lastly, it is my most pleasant duty to express my indebtedness Professors W. Langner (Schmalenbeck), P. Maheshwari (Delhi) and P. N. Mehra (Chandigarh) for their continued encouragement and advice. To Dr. M. L. Stiff (Lafayette), I am deeply grateful for allowing me to quote his valuable unpublished work on the cytology of conifers.

Table of Chromosome Numbers

Species	Chromosome number n	Chromosome number 2n	Reference
I. CYCADALES			
1. Cycadaceae			
Cycas (x=11)			
circinalis	—	22	SAX and BEAL, 1934.
revoluta	—	22	SAX and BEAL, 1934.
	—	22, 24	NAKAMURA, 1929
rumphii	—	22	SAX and BEAL, 1934.
Bowenia (x=9)			
serrulata	—	18	SAX and BEAL, 1934.
spectabilis	—	18	RESENDE and RIJO, 1948.
Macrozamia (x=9)			
miquelii	—	18	SAX and BEAL, 1934.
moorei	—	18	SAX and BEAL, 1934.
tridentata	—	18	SAX and BEAL, 1934.
Stangeria (x=8)			
paradoxa	—	16	SAX and BEAL, 1934.
Encephalartos (x=8 [?], 9)			
altensteinii	—	16	SAX and BEAL, 1934.
	—	18	RESENDE, 1940.
barteri	9	—	BERRIE, 1959.
caffer	—	18	VIVEIROS, 1951.
cycadifolius	—	ca. 18	RESENDE and RIJO, 1948.
horridus	—	18	RESENDE, 1940.
latifrons	—	18	RESENDE, 1940.
lehmanii	—	18	VIVEIROS, 1951.
villosus	—	18	VIVEIROS, 1951.
Dioon (x=9)			
edule	—	18	VIVEIROS, 1951.
spinulosum	—	18	SAX and BEAL, 1934.
Microcycas (x=13)			
calcoma	—	26	SAX and BEAL, 1934.
Ceratozamia (x=8)			
mexicana	—	16	SAX and BEAL, 1934.
Zamia (x=8, 9)			
floridana	—	16	SAX and BEAL, 1934.
loddigesii	—	18	RESENDE and RIJO, 1948.
media	—	16	SAX and BEAL, 1934.
II. GINKGOALES			
2. Ginkgoaceae			
Ginkgo (x=12)			
biloba	12	24	SAX and SAX, 1933; RESENDE and RIJO, 1948; TANAKA et al, 1952; LEE, 1954; NEWCOMER, 1954; POLLOCK, 1957; CZEIKA and SCHIMAN, 1960.
III. CONIFERALES			
3. Araucariaceae			
Araucaria (x=13)			
angustifolia (brasiliana)	—	26	FLORY, 1936; STIFF, 1952.
bidwilli	—	26	FLORY, 1936.
cunninghamii	—	26	FLORY, 1936.
excelsa	—	26	STIFF, 1952.
Agathis (x=13)			
alba	—	26	ZINNAI, 1948.
australis	13	26	HAIR and BEUZENBERG, 1958b.
brownii (robusta)	—	26	FLORY, 1936.
species	—	26	FLORY, 1936.
4. Podocarpaceae			
Phyllocladus (x=9)			
alpinus	9	18	HAIR and BEUZENBERG, 1958a, b.
glaucus	9	18	HAIR and BEUZENBERG, 1958a, b.
trichomanoides	9	18	HAIR and BEUZENBERG, 1958a, b.
Pherosphaera (x=13)			
hookeriana	13	26	HAIR and BEUZENBERG, 1958a.
fitzgeraldi	13	26	HAIR and BEUZENBERG, 1958a.
Microcachrys (x=15)			
tetragona	15	30	HAIR and BEUZENBERG, 1958a.
Saxegothaea (x=12)			
conspicua	12	24	HAIR and BEUZENBERG, 1958a.
Acmopyle (x=10)			
pancheri	10	20	HAIR and BEUZENBERG, 1958a.
Dacrydium (x=9-12, 15)			
araucarioides	10	20	HAIR and BEUZENBERG, 1958a
balansae	10	20	HAIR and BEUZENBERG, 1958a.
bidwillii	9	18	HAIR and BEUZENBERG, 1958a, b.
biforme	12	24	HAIR and BEUZENBERG, 1958a, b.
colensoi	10	20	HAIR and BEUZENBERG, 1958a, b.
cupressinum	10	20	HAIR and BEUZENBERG, 1958a, b.
elatum	10	20	HAIR and BEUZENBERG, 1958a.
franklinii	15	30	HAIR and BEUZENBERG, 1958a.
guillauminii	10	20	HAIR and BEUZENBERG, 1958a.
intermedium	15	30	HAIR and BEUZENBERG, 1958a, b.
kirkii	11	22	HAIR and BEUZENBERG, 1958a, b.
laxifolium	15	30	HAIR and BEUZENBERG, 1958a, b.
lycopodioides	10	20	HAIR and BEUZENBERG, 1958a.
taxoides	10	20	HAIR and BEUZENBERG, 1958a.
Podocarpus (x=10-13, 17-19)			
Section 1. *Dacrycarpus*			
dacrydioides	10	20	HAIR and BEUZENBERG, 1958a, b.

Species	Chromosome number		Reference
	n	2n	
imbricatus	10	20	HAIR and BEUZENBERG, 1958a.
vieillardii	10	20	HAIR and BEUZENBERG, 1958a.
Section 2. *Microcarpus*			
ustus	18	36	HAIR and BEUZENBERG, 1958a.
Section 3. *Nageia*			
blumei	10	20	HAIR and BEUZENBERG, 1958a.
nagi	13	26	HAIR and BEUZENBERG, 1958a.
	12	24	ISHIKAWA, 1916; STIFF, 1952.
Section 4. *Afrocarpus*			
falcatus	12	24	FLORY, 1936; MEHRA and KHOSHOO, 1956b; HAIR and BEUZENBERG, 1958a.
gracilior	12	24	MEHRA and KHOSHOO, 1956b; HAIR and BEUZENBERG, 1958a.
Section 5. *Polypodiopsis*			
comptonii	10	20	HAIR and BEUZENBERG, 1958a.
minor	10	20	HAIR and BEUZENBERG, 1958a.
palustris	10	20	HAIR and BEUZENBERG, 1958a.
vitiensis	10	20	HAIR and BEUZENBERG, 1958a.
Section 6. *Sundacarpus*			
amarus	19	38	HAIR and BEUZENBERG, 1958a.
Section 7. *Stachycarpus*			
Subsection A. *Euprumnopitys*			
andinus	19	38	FLORY, 1936; HAIR and BEUZENBERG, 1958a.
ferrugineus	18	36	HAIR and BEUZENBERG, 1958a, b.
spicatus	19	38	HAIR and BEUZENBERG, 1958a, b.
Section 8. *Eupodocarpus*			
Subsection A.			
elongatus	—	24	STIFF, 1952.
	11	22	HAIR and BEUZENBERG, 1958a.
henkelii	10, 11	20, 22	HAIR and BEUZENBERG, 1958a.
	11	22	MEHRA and KHOSHOO, 1956b*).
latifolius	10	20	HAIR and BEUZENBERG, 1958a.

*) These authors worked this species under the name *P. latifolius* from the material collected from Forest Research Institute, Dehra Dun (India). However, Dr. NETTA E. GRAY is of the opinion that these plants are actually *P. henkelii*.

Species	Chromosome number		Reference
	n	2n	
Subsection B.			
elatus	—	34—36	HAIR and BEUZENBERG, 1958a.
macrophyllus	19	38	FLORY, 1936; TAHARA, 1941; MEHRA and KHOSHOO, 1956b.
neriifolius	—	38	FLORY, 1936.
	—	33	HAIR and BEUZENBERG, 1958a.
novae-caledoniae	—	37	HAIR and BEUZENBERG, 1958a.
polystachyus	—	33	HAIR and BEUZENBERG, 1958a.
Subsection C.			
salignus	19	38	STIFF, 1952; HAIR and BEUZENBERG, 1958a.
Subsection D.			
acutifolius	—	38	STIFF, 1952.
	17	34	HAIR and BEUZENBERG, 1958a, b.
alpinus	19	38	STIFF, 1952.
hallii	17	34	HAIR and BEUZENBERG, 1958a, b.
nivalis	19	38	SNOAD, 1952; STIFF, 1952; HAIR and BEUZENBERG, 1958a, b.
var. *erectus* (*nivalis* × *hallii*)	$2_{III}+15_{II}$	36	HAIR and BEUZENBERG, 1958a, b.
totara	17	34	HAIR and BEUZENBERG, 1958a, b.
Subsection F.			
longefoliolatus	—	37, 38	HAIR and BEUZENBERG, 1958a.
5. Cephalotaxaceae			
Cephalotaxus (x=12)			
drupacea	12	—	SUGIHARA, 1940; MEHRA and KHOSHOO, 1956b.
var. *pedunculata*	12	24	STIFF, 1952; KHOSHOO, 1957a, b.
fortunei	12	—	SAX and SAX, 1933.
6. Taxaceae			
Amentotaxus (x=11)			
argotaenia	11	—	SUGIHARA, 1943b.
Torreya (x=11)			
*macrosperma**	11	—	NAKAJIMA, 1942.
nucifera	11	—	TAHARA, 1940a; HIRAYOSHI, 1942; HIRAYOSHI and NAKAMURA, 1942.
Taxus (x=12)			
baccata (*wallichiana*)	12	24	DARK, 1932; SAX and SAX, 1933; SUGIHARA, 1946; STIFF, 1952.
canadensis	12+1B	–	DARK, 1932.
	12	—	SAX and SAX, 1933.

Species	Chromosome number n	Chromosome number 2n	Reference
cuspidata	12	24	Dark, 1932; Sax and Sax 1933.
hunnewelliana	12	—	Sax and Sax, 1933.
media	12	—	Sax and Sax, 1933.
7. Pinaceae			
Keteleeria (x=12)			
davidiana (evelyniana)	12	—	Sugihara, 1943a; Wang, 1948.
Abies (x=12)			
balsamea	12	—	Miyake, 1903.
cephalonica	12	—	Sax and Sax, 1933.
concolor	12	—	Sax and Sax, 1933.
magnifica	—	24	Stiff, 1952.
nordmanniana	12	—	Sax and Sax, 1933.
pindrow	12	—	Mehra and Khoshoo, 1956a.
veitchii	12	—	Sax and Sax, 1933.
Pseudotsuga (x=13)			
douglasii	—	24(?)	Durrieu-Vabre, 1958.
taxifolia	13	—	Sax and Sax, 1933; Zenke, 1953.
Tsuga (x=12)			
canadensis	12	—	Sax and Sax, 1933.
caroliniana	12	—	Sax and Sax, 1933.
diversifolia	12	—	Sax and Sax, 1933.
Picea (x=12)			
abies	12	24	Sax and Sax 1933; Andersson, 1947
	—	24, ±28, 36, 48	Kiellander, 1950.
	—	24, 28—30, 30—36, 36, 37, 48, 60—70	Illies, 1953, 1958.
asperata	12	—	Santamour, 1960.
bicolor	12	—	Santamour, 1960.
engelmannii	12	—	Santamour, 1960.
glauca	12	24	Sax and Sax, 1933; Stiff, 1952.
jezoensis	12	—	Santamour, 1960.
koyamai	12	—	Santamour, 1960.
likiangensis (balfouriana)	12	—	Santamour, 1960.
mariana	12	—	Sax and Sax, 1933.
mariana×glauca	12	—	Little and Pauley, 1958.
maximowiczii	12	—	Santamour, 1960.
montigena	12	—	Santamour, 1960.
omorika	12	—	Santamour, 1960.
orientalis	12	—	Santamour, 1960.
pungens	12	—	Sax and Sax, 1933.
rubens	12	—	Santamour, 1960.
sitchensis	—	24	Thomas, 1945.
smithiana	12	—	Mehra and Khoshoo, 1956a.
Cedrus (x=12)			
atlantica	—	24	Stiff, 1952.
deodara	12	—	Mehra and Khoshoo, 1956a.
libani	12	—	Sax and Sax, 1933.
Larix (x=12)			
decidua (europaea)	12	—	Sax and Sax, 1933.
	—	24, 48	Christiansen, 1950.
decidua×occidentalis	—	36	Syrach Larsen and Westergaard, 1938; Knaben, 1953.
eurolepis	12	—	H. J. Sax, 1932.
gmelinii (dahurica)	—	24	Woycicki, 1906.
	—	36	Manžos and Pozdnjakov, 1960.
leptolepis (kaempferi)	12	—	Sax and Sax, 1933.
occidentalis	12	—	Sax and Sax, 1933.
*polonica**	—	24	Hruby, 1933.
sibirica	—	24	Kiellander, 1948.
*sudetica**	—	24	Hruby, 1933.
Pseudolarix (x=12)			
amabilis	22	44	Sax and Sax 1933; Stiff, 1952.
Pinus (x=12)			
armandi	12	24	Stiff, 1952; Santamour, 1960.
ayacahuite	12	—	Santamour, 1960.
banksiana	12	24	Sax and Sax, 1933; Stiff, 1952.
bungeana	12	—	Sax and Sax, 1933.
canariensis	—	24	Bowden, 1945; Mehra and Khoshoo, 1956a.
caribaea	—	24	Mehra and Khoshoo, 1956a.
as *elliottii*	—	24, 36, 48	Mergen, 1958.
cembra	12	—	Santamour, 1960.
cembroides (edulis)	12	24	Stiff, 1952; Santamour, 1960.
clausa	—	24	Stiff, 1952.
contorta	—	24	Langlet, 1934.
densiflora	12	—	Hirayoshi, 1942; Hirayoshi and Nakamura, 1942.
	—	24, 48	Zinnai, 1952.
densiflora×thunbergii	12	—	Hirayoshi, Nakamura and Kano, 1943.
echinata	12	—	Sax and Sax, 1933.
flexilis	12	—	Sax and Sax, 1933.
gerardiana	—	24	Mehra and Khoshoo, 1956a.
halepensis	—	24	Mehra and Khoshoo, 1956a.
jeffreyi	12	24	Sax and Sax, 1933; Stiff, 1952.
khasya	—	24	Mehra and Khoshoo, 1956a.
koraiensis	12	—	Santamour, 1960.
lambertiana	—	24	Mehra and Khoshoo, 1956a.
luchuensis	—	24	Shibata et al, 1955.
massoniana	—	24	Stiff, 1952.

Species	Chromosome number n	Chromosome number 2n	Reference
merkusii	12	—	Mehra and Khoshoo, 1956a.
montezumae	—	24	Stiff, 1952.
monticola	12	—	Santamour, 1960.
mugo	12	24	Sax and Sax, 1933; Stiff, 1952.
nigra	12	24	Sax and Sax, 1933; Mehra and Khoshoo, 1956a.
palustris	—	24	Mathews, 1932.
parviflora	12	—	Sax and Sax, 1933.
patula	—	24	Bowden, 1945.
peuce	12	24	Sax and Sax, 1933; Stiff, 1952.
pinaster	—	24	Mehra and Khoshoo, 1956a.
pinea	—	24	Stiff, 1952; Lane, 1955.
ponderosa	12	24	Sax and Sax, 1933; Mehra and Khoshoo, 1956a.
pungens	—	12	Sax and Sax, 1933.
radiata	—	24	Mehra and Khoshoo, 1956a.
	—	24, 48	Rodger, 1953—54.
resinosa	12	—	Sax and Sax, 1933.
rigida	12	—	Sax and Sax, 1933.
roxburghii	12	24	Sethi, 1928; Mehra and Khoshoo,1956a.
sabiniana	—	24	Stiff, 1952.
strobus	12	—	Sax and Sax, 1933.
sylvestris	12	24	Sax and Sax, 1933; Stiff, 1952.
tabulaeformis	12	—	Sax and Sax, 1933.
taeda	—	24	Shibata et al, 1955.
thunbergii	12	24	Sax and Sax, 1933; Stiff, 1952.
virginiana	12	—	Sax and Sax, 1933; Stiff, 1952.
wallichiana (griffithii)	12	24	Mehra and Khoshoo, 1956a; Santamour, 1960.

8. Sciadopityaceae

Species	n	2n	Reference
Sciadopitys (x=10)			
verticillata	10	20	Sax and Beal, 1934; Tahara, 1937, 1940b; Hirayoshi, 1942; Hirayoshi and Nakamura, 1942.

9. Taxodiaceae

Species	n	2n	Reference
Cunninghamia (x=11)			
konishii	11	22	Hirayoshi and Nakamura, 1942; Stiff, 1952.
lanceolata	11	22	Sugihara, 1941a; Mehra and Khoshoo, 1956a.
Taiwania (x=11)			
cryptomerioides	11	22	Sugihara, 1941b; Stiff, 1952.
Athrotaxis (x=11)			
cupressoides	11	22	Gulline, 1952.
laxifolia	11	22	Gulline, 1952.
selaginoides	11	22	Gulline, 1952.
Cryptomeria (x=11)			
japonica	11	22	Sax and Sax, 1933; Mehra and Khoshoo, 1956a.
	—	22, 33, 44	Chiba, 1950; Zinnai and Chiba, 1951; Saito and Hashizume, 1958.
Taxodium (x=11)			
distichum	—	22	Stebbins, 1948.
mucronatum	—	22	Mehra and Khoshoo, 1956a.
Metasequoia (x=11)			
glyptostroboides	—	22	Stebbins, 1948.
Sequoiadendron (x=11)			
giganteum	—	22	Buchholz, 1939; Jensen and Levan, 1941.
Sequoia (x=11)			
sempervirens	33	66	Hirayoshi and Nakamura, 1943; Stebbins, 1948; Stiff, 1952.

10. Cupressaceae

Species	n	2n	Reference
Actinostrobus (x=11)			
pyramidalis	—	22	Mehra and Khoshoo, 1956a.
Callitris (x=11)			
calcarata	—	22	Mehra and Khoshoo, 1956a.
cupressiformis	—	22	Mehra and Khoshoo, 1956a.
glauca	—	22	Mehra and Khoshoo, 1956a.
morrisoni	—	22	Mehra and Khoshoo, 1956a.
propinqua	—	22	Mehra and Khoshoo, 1956a.
robusta	—	22	Mehra and Khoshoo, 1956a.
verrucosa	—	22	Mehra and Khoshoo, 1956a.
Widdringtonia (x=11)			
cupressoides	—	22	Mehra and Khoshoo, 1956a.
Libocedrus (x=11)			
bidwillii	11	22	Hair and Beuzenberg, 1958b.
chilensis	—	22	Stiff, 1952; Hunziker, 1958.
plumosa	11	22	Lane, 1955; Hair and Beuzenberg, 1958b.

Species	Chromosome number		Reference
	n	2n	
Tetraclinis (x=11)			
articulata	—	22	MEHRA and KHOSHOO, 1956a.
Cupressus (x=11)			
arizonica	11	22	MEHRA and KHOSHOO, 1956a; HUNZIKER, 1958.
cashmeriana	11	—	MEHRA and KHOSHOO, 1956a.
dupreziana	11	—	QUÉZEL, 1955.
forbesii	—	22	STIFF, 1952.
funebris	11	22	MEHRA and KHOSHOO, 1956a; HUNZIKER, 1958.
glabra	—	23	HUNZIKER, 1958.
lusitanica	11	22	CÂMARA and DE JESUS, 1946; MEHRA and KHOSHOO, 1956a; HUNZIKER, 1958.
macnabiana	—	22	STIFF, 1952.
macrocarpa	—	22	STIFF, 1952; HUNZIKER, 1958.
sempervirens	—	22	MEHRA and KHOSHOO, 1956a; HUNZIKER, 1958.
torulosa	11	22	MEHRA and KHOSHOO, 1956a; HUNZIKER, 1958.
Chamaecyparis (x=11)			
lawsoniana	11	—	SAX and SAX, 1933.
obtusa	11	22	HIRAYOSHI, 1942; HIRAYOSHI and NAKAMURA, 1942; SHIBATA et al, 1955.
pisifera	11	—	SUGIHARA, 1938; STIFF, 1952.
var. *pisifera*	—	20	SHIBATA et al, 1955.
var. *squarrosa*	—	22	SHIBATA et al, 1955.
× *Cupressocyparis* (x=11)			
leylandii	—	22	STIFF, 1952.
Thujopsis (x=11)			
dolabrata	11	—	SUGIHARA, 1939.
Thuja (x=11)			
occidentalis	11	22	SAX and SAX, 1933; MEHRA and KHOSHOO, 1956a.
plicata	11	—	SAX and SAX, 1933.
standishii	11	—	SAX and SAX, 1933.
Biota (x=11)			
orientalis (Thuja orientalis)	11	22	SAX and SAX, 1933; MEHRA and KHOSHOO, 1956a.
Juniperus (x=11)			
bermudiana	11	—	MEHRA and KHOSHOO, 1956a.
chinensis pfitzeriana	22	—	SAX and SAX, 1933.

Species	Chromosome number		Reference
	n	2n	
communis	11	22	SAX and SAX, 1933; LÖVE and LÖVE, 1948; JØRGENSEN et al, 1958.
formosana	—	22	STIFF, 1952.
horizontalis	11	22	ROSS and DUNCUN, 1949.
monosperma	—	22	STIFF, 1952.
phoenicea	11	22	STIFF, 1952; MEHRA and KHOSHOO, 1956a.
procera	—	22	MEHRA KHOSHOO, 1956a.
rigida	11	—	SAX and SAX, 1933.
sabina	—	22—24	REESE, 1952.
squamata meyeri	—	44	JENSEN and LEVAN, 1941.
virginiana	11	22	SAX and SAX, 1933; LÖVE and LÖVE, 1948; ROSS and DUNCUN, 1949; MEHRA and KHOSHOO, 1956a.
	—	22, 23	STIFF, 1951, 1952.
virginiana× *horizontalis*	11	22	ROSS and DUNCUN, 1949.
utahensis	—	22	STIFF, 1952.

IV. EPHEDRALES

11. Ephedraceae

Species	n	2n	Reference
Ephedra (x=7)			
altissima	14	28	RESENDE, 1937; MEHRA, 1946.
americana	7	14	FLORIN, 1932; RESENDE, 1937; HUNZIKER, 1955.
as *andina*	—	14, 28, 30	HUNZIKER, 1953, 1955.
as *rupestris*	—	14	KRAPOVICKAS 1954; HUNZIKER, 1955.
breana	—	14, 28	HUNZIKER, 1953, 1955; KRAPOVICKAS, 1954.
distachya	—	28	FLORIN, 1932; RESENDE, 1937.
equisetina	—	14	FLORIN, 1932.
foliata	7	—	MEHRA, 1946.
fragilis (campylopoda)	7	—	GEITLER, 1929.
frustillata	—	14	KRAPOVICKAS, 1954; HUNZIKER, 1955.
gerardiana	7	—	MEHRA, 1946.
intermedia	14	28	MEHRA, 1946.
likiagensis	14	—	MEHRA, 1946.
multiflora	—	14	KRAPOVICKAS, 1954; HUNZIKER, 1955.
nebrodensis (major)	7	14	GEITLER, 1929; FLORIN, 1932; MARTINEZ VAZQUEZ, 1959.
ochreata	—	14	KRAPOVICKAS, 1954; HUNZIKER, 1955.

Species	Chromosome number		Reference
	n	2n	
saxatilis	14	—	MEHRA, 1946.
sinica	14	28	RESENDE, 1937; MEHRA, 1946.
triandra	7	14	HUNZIKER, 1953, 1955; KRAPOVICKAS, 1954.
tweediana	7	14	HUNZIKER, 1953, 1955; KRAPOVICKAS, 1954.
V. WELWITSCHIALES			
12. Welwitschiaceae			
Welwitschia (x=21)			
mirabilis	—	42	FLORIN, 1932.
	—	42, 84	FERNANDES, 1936.
VI. GNETALES			
13. Gnetaceae			
Gnetum (x=22)			
gnemon	22	—	FAGERLIND, 1941.
ula	22	—	MEHRA and RAI, 1957.

Summary

This paper consolidates the information on the chromosome numbers of 264 species (42%) and some hybrids in the gymnosperms. The investigated species belong to 55 genera (82%) covering all the 13 living families of the group. This leaves nearly 387 species and 12 genera totally unworked. The latter urgently need a cytological study. After reviewing the recent important cytological contributions, the writer has put forward some suggestions for future work. It is requested that omissions, if any, may be pointed out to the writer so that the list becomes complete and up-to-date. Furthermore, he will feel deeply grateful to anyone who can send him viable seeds of any species of the totally unworked or the partially worked out genera listed in the first part of the paper.

Zusammenfassung

Titel der Arbeit: *Chromosomenzahlen bei Gymnospermen.*

Die vorliegende Publikation faßt die Kenntnisse über die Chromosomenzahlen von 264 Spezies (42%) und einigen Hybriden bei den Gymnospermen zusammen. Die untersuchten Arten gehören 55 Gattungen (82%) an und entstammen allen der 13 lebenden Familien dieser Gruppe. Es bleiben dabei etwa 387 Spezies und 12 Gattungen vollständig unbearbeitet, die noch unbedingt zytologisch untersucht werden müssen. Nach einem Überblick über wichtige neuere zytologische Beiträge macht Verfasser Vorschläge für künftige Arbeiten. Es wird gebeten, womöglich vorhandene Lücken dem Autor mitzuteilen, damit die Liste vervollständigt werden kann. Ferner wäre er sehr dankbar für keimfähige Samenproben von den Arten aus den Gattungen des ersten Teils der Arbeit, die bisher noch vollständig unbearbeitet geblieben oder nur teilweise untersucht worden sind.

Résumé

Titre de l'article: *Nombres chromosomiques chez les Gymnospermes.*

Cet article confirme et vérifie les renseignements sur les nombres chromosomiques de 264 espèces (42%) et quelques hybrides de Gymnospermes. Les espèces étudiées appartiennent à 55 genres (82%) appartenant à l'ensemble des 13 familles du groupe qui existe actuellement. 387 espèces et 12 genres n'ont pas été étudiés. L'étude cytologique paraît tout à fait nécessaire. Après avoir passé en revue les publications récentes et importantes sur ce sujet, l'auteur fait des propositions pour les travaux futurs. Si certaines omissions sont remarquées, l'auteur souhaite qu'elles lui soient signalées afin qu'il puisse compléter et mettre à jour cette liste. De plus, il sera profondément reconnaissant à ceux qui pourront lui envoyer des graines viables de toutes les espèces appartenant aux genres qui, d'après la première partie de l'article, n'ont fait l'objet d'aucune étude ou ont été incomplètement explorés.

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