CYTOLOGY OF CONIFERS. I

By P. N. MEHRA and T. N. KHOSHOO

Botany Department, Panjab University, Amritsar, India

(With Plate 5 and Thirty-seven Text-figures)

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Some important contributions have appeared on the cytology of Gymnosperms in recent years. Sax & Sax (1933) published their investigations on fifty-three species belonging to sixteen genera of the Coniferales. In this paper was also included the sole survivor of the Ginkgoales—*Ginkgo biloba*. This was followed a year later by an equally comprehensive survey on all the genera of Cycadales by Sax & Beal (1934). In 1936 Flory worked out both the genera of Araucariaceae and a few species of *Podocarpus*. Stebbins (1948) published the cytological situation in *Sequoia sempervirens* and *Metasequoia*—the recently discovered genus of Taxodiaceae. In 1952 Tanaka, Takemasa & Sinoto published a karyotype analysis of *Ginkgo biloba*. This species has also been simultaneously worked out by Newcomer (1954) and Lee (1954). In Gnetales the first serious contribution came from Geitler (1929) on the genus *Ephedra*, followed by Florin (1932) on some species of the same genus and also on the monotypic *Welwitschia*. In 1946 Mehra made a detailed study of karyotypes of seven species of *Ephedra* with particular emphasis on the formation of the small percentage of diploid sex cells in nature. Hunziker (1953) and Fuchs (1954) have studied some more species of the genus. The only reliable report of the chromosome number of *Gnetum* is by Fagerlind (1941), who counted 22 bivalents in *G. gnemon*. Most of the other cytological work on Gymnosperms has been incidental to morphological and embryological studies and has not been referred here.

MATERIAL AND METHODS

It was originally intended to study the cytology of Indian conifers only, but as the work progressed material of some foreign species became available and these have also been included. In all, forty-one species belonging to fourteen genera have been included in this paper. These belong to Abietaceae, Taxodiaceae and Cupressaceae.

Species names have been followed as given in Dallimore & Jackson (1948). For the distribution of the various species the reader is referred to the same book. The source of each species used in the present investigation is given in Table 1, column 5.

Root-tips of germinating seeds were mostly used, but in some cases studies were carried out on female gametophytes, young leaves and shoot apices. Seeds of the various species were sown in sawdust in winter months.

It is well known that conifers possess long chromosomes which present considerable difficulty in exact analysis when dealing with somatic tissues. Previous investigators like Sax & Sax (1933), Sax & Beal (1934) and Flory (1936) depended upon physical pressure on the cells in macerated preparations to scatter the chromosomes for obtaining clear preparations. At that time the effect of the alkaloid colchicine was not known. In the present investigation the material was pretreated with colchicine, α-Bromo-naphthalene or 8-Oq., or simply a cold shock was given before squashing. This enabled the chromosomes to shorten and to scatter, giving precise and clear pictures of their morphology.

The material was either fixed in Craf and stained in Schiff's reagent or was directly stained in any of the stain fixatives containing macerating agent. Microsporangia were either smeared, fixed in Craf and stained with iodine-crystal violet or squashed in iron acetocarmine.

All diagrams were made to give an approximate magnification of × 3000 which has been reduced to half in publication. Chromosomes of a few species have been separated in drawing for clarity.

No attempt has been made to compare the size of the chromosomes of the various species, since no uniform technique has been followed. Where the two arms of a chromosome are unequal and the shorter arm is half or more than half the length of the longer one, the chromosome has been placed in the median-submedian category. If the shorter arm is distinctly smaller than one-half of the longer arm the chromosome has been designated as subterminal. In critical cases actual measurements were undertaken to decide the morphology of the chromosome.

OBSERVATIONS

Abietaceae

Pinus

The following twelve species have been investigated from root-tips: *Pinus canariensis* C. Smith (Text-fig. 1), *P. caribaea* Morlet (Text-fig. 2), *P. gerardiana* Wallich (Text-fig. 3 and Pl. 5, fig. 1), *P. halepensis* Miller (Text-fig. 4), *P. khasya* Royle (Text-fig. 5), *P. lambertiana* Douglas (Text-fig. 6), *P. nigra* Arnold (*P. laricio* Poiret) (Text-fig. 7), *P. pinaster* Aiton (Text-fig. 8), *P. ponderosa* Douglas (Text-fig. 9), *P. radiata* D. Don (*P. insignis* Douglas) (Text-fig. 10), *P. roxburghii* Sarg. (*P. longifolia* Roxb.) (Text-fig. 11) and *P. wallichiana* Jack (*P. excelsa* Wallich) (Text-fig. 12). In *P. merkusii* Jungh & de Vriese (Text-fig. 13) 12 bivalents were counted in pollen mother cells.

Of the above species previous records of chromosome number are known for four only. Sethi (1928) counted 12 bivalents in pollen mother cells in *P. roxburghii*. Sax & Sax (1933) reported the same number in *P. nigra* and *P. ponderosa*. Bowden (1945) found 24 chromosomes in root-tips of *P. canariensis*.

Twenty-four is the diploid chromosome number in all the twelve species. The chromosomes have either a median or submedian centromere. The various species differ in number and location of secondary constrictions (see Table 1). Eight chromosomes of *P. gerardiana* (Text-fig. 3 and Pl. 5, fig. 1) possess secondary constrictions, six of which are subterminal in position, while the remaining two are nearly median in one of the arms. Six secondarily constricted chromosomes are present in *P. lambertiana* (Text-fig. 6) and *P. roxburghii* (Text-fig. 11). In both these the constrictions are subterminal. *P. wallichiana* (Text-fig. 12) also possesses the same number, but only four secondary constrictions are subterminal and the remaining two are very near the primary constrictions. Of the four subterminal constrictions two cut a relatively shorter distal segment. In *P. khasya*

(Text-fig. 5) and *P. radiata* (Text-fig. 10) there are four secondary constrictions. In the former all are situated near the centromere, while in the latter they cut a knob-like distal segment. Only three chromosomes of *P. canariensis* (Text-fig. 1) were observed with subterminal secondary constrictions. Since it is a diploid complement one would expect four such chromosomes, and it is possible that the fourth may have been overlooked. Only two chromosomes have secondary constrictions in *P. caribaea* (Text-fig. 2). These are situated close to the centromere. In the remaining four species no secondary constrictions were observed in our preparations.

Sax & Sax (1933) worked out fourteen species of the genus. They have not reported any secondary constrictions or satellites in any of the species of the genus, perhaps because they did not work from this angle. The basic karyotype described by them is, however, the same as described above.

Cedrus

In *Cedrus deodara* Loudan the haploid chromosome number as determined from the cells of the female gametophyte is 12 (Text-fig. 14). One of these has a subterminal, while the rest have median or submedian centromeres. In one of the latter chromosomes there is a secondary constriction situated in the middle of one of the arms.

The same number and morphology of the chromosomes has been reported by Sax & Sax in *C. libanotica*, except for any reference to the secondary constriction.

Picea

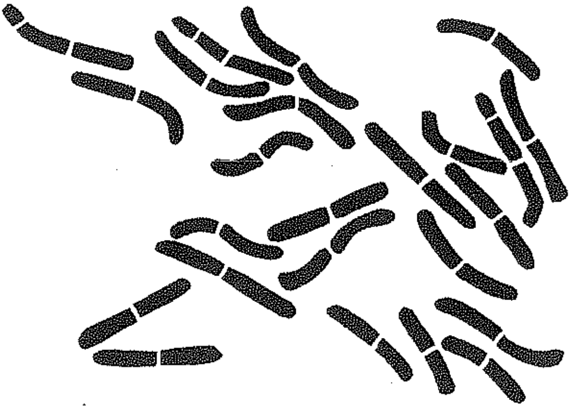
The female gametophyte of *Picea smithiana* (Wallich) Boiss (*P. morinda* Link) revealed 12 chromosomes (Text-fig. 15). Three have a subterminal, and the remaining nine have a median-submedian centromere. One of the former and two of the latter bear a subterminal secondary constriction each.

Similar morphology of chromosomes is recorded by Sax & Sax in *P. abies* and *P. pungens*. These authors did not mention the secondary constrictions.

Abies

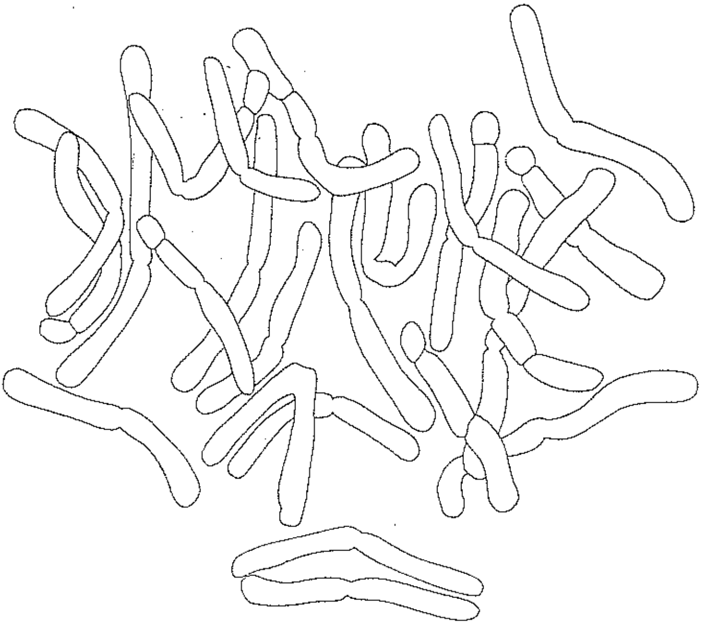
Abies pindrow Spach possesses 12 chromosomes in the female gametophyte cells. Five of the chromosomes possess a subterminal and seven have a median-submedian centromere (Text-fig. 16). Two of the latter chromosomes bear a subterminal secondary constriction each.

A. cephalonica and *A. concolor* have the same morphology (Sax & Sax, 1933). No secondary constrictions have been reported in these.

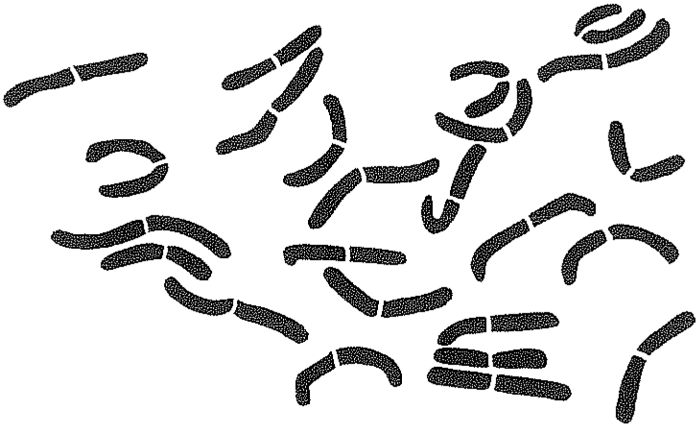


Text-fig. 1. *Pinus canariensis*, $2n=24$.

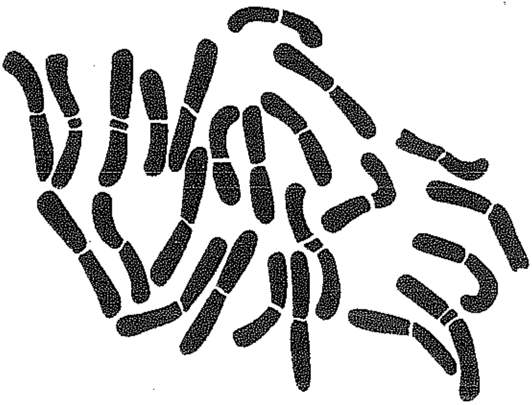
Text-fig. 2. *P. caribaea*, $2n=24$.



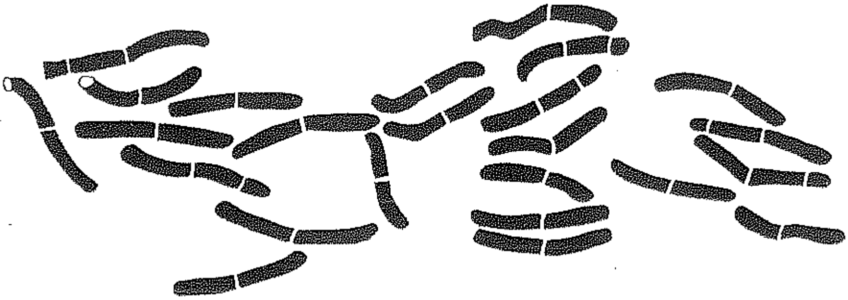
Text-fig. 3. *P. gerardiana*, $2n=24$.



Text-fig. 4. *P. halepensis*, $2n=24$.

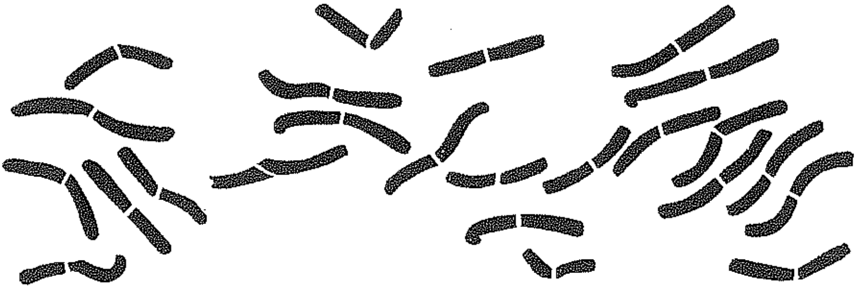


Text-fig. 5. *P. khasya*, $2n=24$.

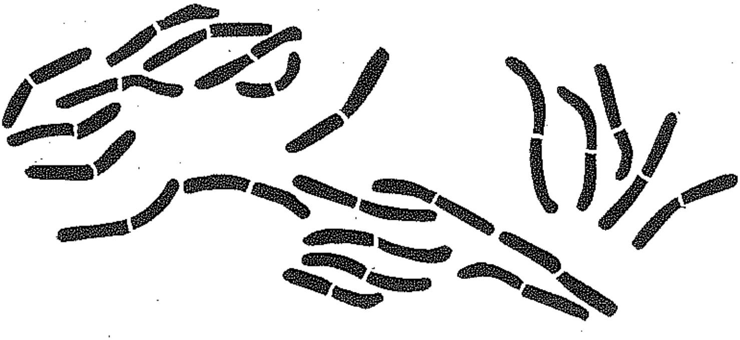


Text-fig. 6. *P. lambertiana*, $2n=24$.

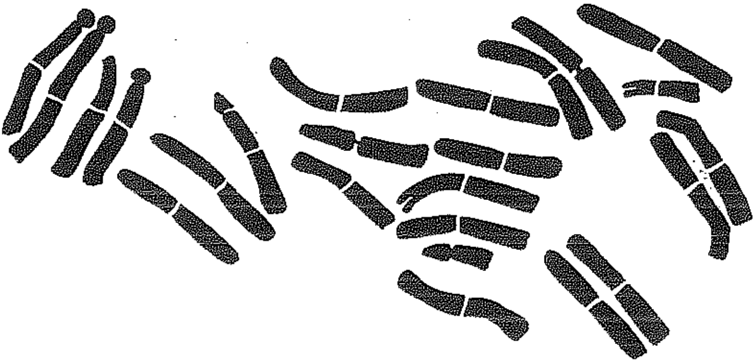
Text-fig. 7. *P. nigra*, $2n = 24$.



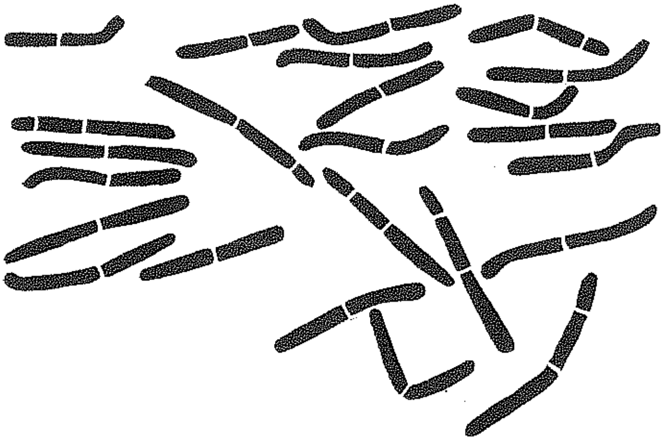
Text-fig. 8. *P. pinaster*, $2n = 24$.



Text-fig. 9. *P. ponderosa*, $2n = 24$.

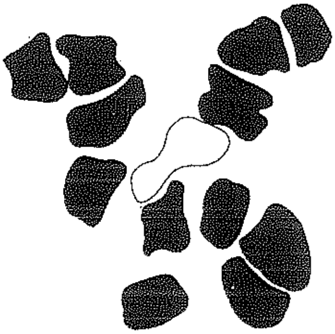


Text-fig. 10. *P. radiata*, $2n = 24$.

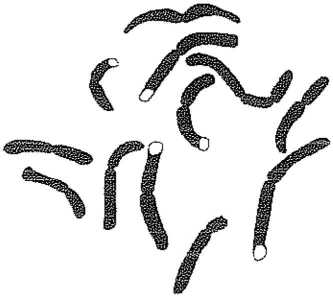


Text-fig. 11. *P. roxburghii*, $2n=24$.

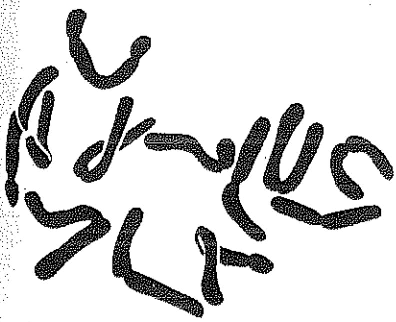
Text-fig. 12. *P. wallichiana*, $2n=24$.



Text-fig. 13. *P. merkusii*, $n=12$, diakinesis, nucleolus unshaded.



Text-fig. 14. *Cedrus deodara*, $n=12$.



Text-fig. 15. *Picea smithiana*, $n=12$.

Text-fig. 16. *Abies pindrow*, $n=12$.

Taxodiaceae

Cunninghamia

Cunninghamia lanceolata (Lamb) Hook. (*C. sinensis* Richard) possesses 22 chromosomes in root-tips (Text-fig. 17). All these have median-submedian centromeres. Two of the chromosomes bear secondary constrictions and two others possess a tandem satellite each.

Eleven bivalents have been counted by Sugihara (1941) in pollen mother cells of this species.

Cryptomeria

Cryptomeria japonica (Linn.) Don. (Text-fig. 18) has 22 chromosomes in the root-tips which are median or submedian. Two pairs have rather inconspicuous secondary constrictions.

Sax & Sax have made similar observations on this species from endosperm tissue.

Taxodium

Taxodium mucronatum Tenore (*T. distichum* Richards var. *mucronatum* Henry) possesses 22 chromosomes in the root-tips of which twenty are median or submedian (Text-fig. 19). One pair is subterminal and has a centromere which is somewhat exaggerated. Two of the former chromosomes bear subterminal secondary constrictions.

Twenty-two chromosomes have been counted by Sax & Sax (1933) and Stebbins (1948) in *T. distichum*.

Cupressaceae

Actinostrobus

Actinostrobus pyramidalis Miquel possesses 22 chromosomes in the root-tips (Fig. 20) which are median or submedian. Two of the chromosomes possess a secondary constriction in a subterminal position.

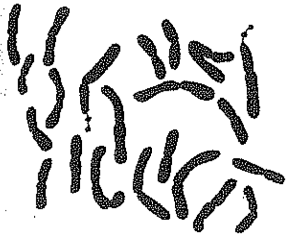
Callitris

The following seven species have been worked out from the root-tips: *Callitris calcarata* R. Brown (Text-fig. 21 and Pl. 5, fig. 2), *C. cupressiformis* Vent (*C. rhomboidea* R. Brown) (Text-fig. 22), *C. glauca* R. Brown (Text-fig. 23), *C. morrisoni* R. T. Baker (Text-fig. 24), *C. propinqua* R. Brown (Text-fig. 25), *C. robusta* R. Brown (Text-fig. 26 and Pl. 5, fig. 3) and *C. verrucosa* R. Brown (Text-fig. 27).

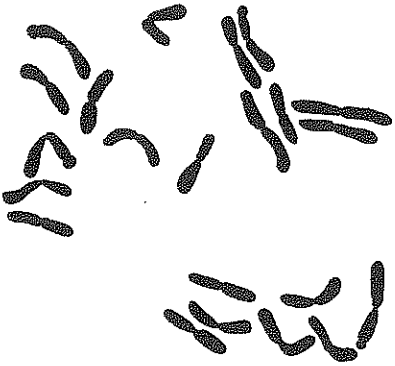
All have essentially the same type of karyotype. There are 22 chromosomes with a median or submedian centromere. Only two have a secondary constriction each. In some it is exaggerated, perhaps due to the effect of 8-O q. The length of the distal segment cut by the secondary constriction is somewhat variable in different species. In *C. cupressiformis*, *C. glauca* and *C. propinqua* there is evidence of some inconspicuous secondary constrictions.

Widdringtonia

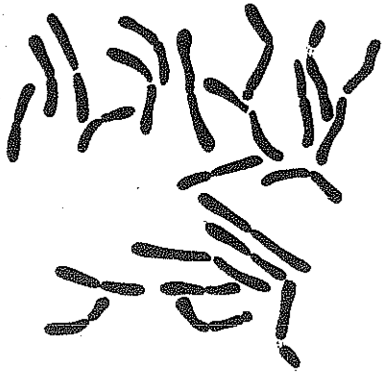
Widdringtonia cupressoides End. possesses 22 chromosomes in the root-tips (Fig. 28), which are median or submedian. A pair of the chromosomes has a rather exaggerated centromere. There are two chromosomes with a subterminal secondary constriction each.



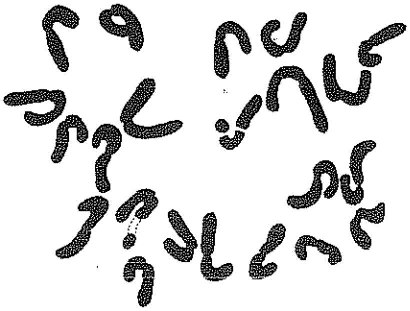
Text-fig. 17. *Cunninghamia lanceolata*, $2n = 22$.



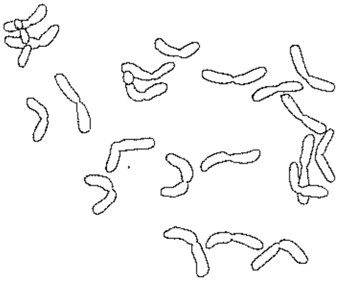
Text-fig. 18. *Cryptomeria japonica*, $2n = 22$.



Text-fig. 19. *Taxodium mucronatum*, $2n = 22$.

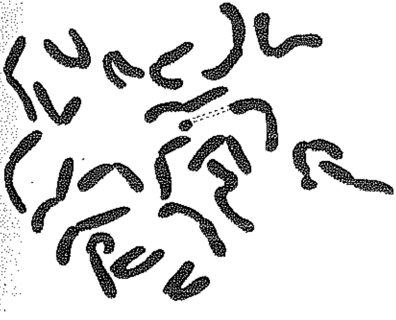


Text-fig. 20. *Actinostrobus pyramidalis*, $2n = 22$.

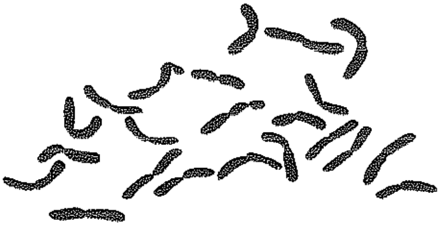


Text-fig. 21. *Callitris calcarata*, $2n = 22$.

Text-fig. 22. *C. cupressiformis*, $2n = 22$.

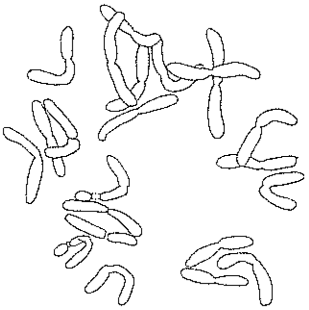


Text-fig. 23. *C. glauca*, $2n = 22$.



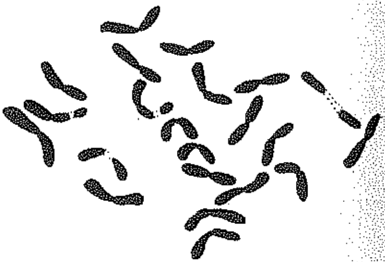
Text-fig. 24. *C. morrisoni*, $2n = 22$.

Text-fig. 25. *C. propinqua*, $2n=22$.



Text-fig. 26. *C. robusta*, $2n=22$.

Text-fig. 27. *C. verrucosa*, $2n=22$.



Text-fig. 28. *Widdringtonia cupressoides*, $2n=22$.

Tetraclinis

Tetraclinis articulata Masters (*Callitris quadrivalvis* Vent) possesses 22 chromosomes as revealed by the squash of a young shoot. All the chromosomes are median or submedian (Text-fig. 29).

Thuja

Thuja orientalis Linn. has 11 chromosomes in endosperm cells (Fig. 30), and the basic karyotype is almost the same as given by Sax & Sax. There is only one chromosome with subterminal centromere, and in the rest it is median or submedian. In the present observations it is noticed that one of the latter chromosomes bears a satellite and another a secondary constriction which is almost median in one of the arms.

T. occidentalis Linn. var. *compacta* Carr. has 22 chromosomes in root-tips. All the chromosomes (Text-fig. 31) have either a median or submedian kinetochore. One pair possesses a secondary constriction almost median in one of the arms. No secondary constrictions have been reported by Sax & Sax in this species.

T. plicata has been investigated by Sax & Sax and has 22 chromosomes.

Cupressus

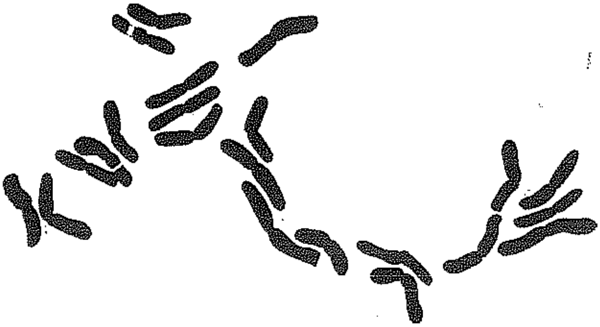
Cupressus funebris Don. (Text-fig. 33) and *C. torulosa* Endlicher (Text-fig. 32) both show 11 chromosomes in endosperm cells. Only one of the chromosomes is subterminal, the rest are median or submedian. One of the median-submedian chromosomes bears a satellite which is somewhat thicker in *C. funebris*. *C. sempervirens* Linn. (Text-fig. 34) possesses

22 chromosomes in root-tips. Two of the chromosomes have a subterminal centromere. The latter bear a secondary constriction in their long arms. Thus all the three species of the genus have the same basic karyotype.

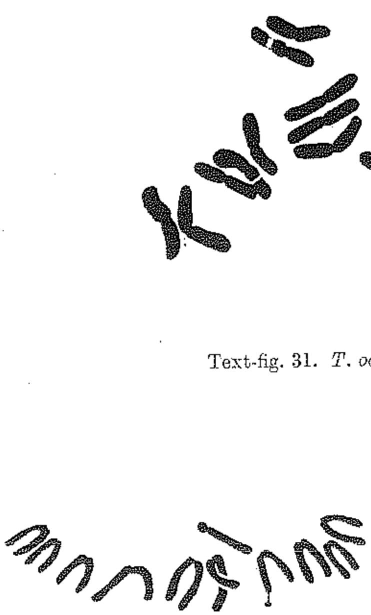
The other three species, namely, *C. cashmeriana* Royle (Text-fig. 35), *C. arizonica* Greene and *C. lusitanica* Miller var. *benthami* Carr. show 11 bivalents in pollen mother cells. Meiosis is perfectly normal in all these species.

Text-fig. 29. *Tetraclinis articulata*, $2n=22$.

Text-fig. 30. *Thuja orientalis*, $n=11$.



Text-fig. 31. *T. occidentalis* var. *compacta*, $2n=22$.



Text-fig. 32. *Cupressus torulosa*, $n=11$.

Text-fig. 33. *C. funebris*, $n=11$.

Text-fig. 34. *C. sempervirens*, $2n=22$.

Text-fig. 35. *C. cashmeriana*, $n=11$, metaphase I.

Juniperus

Juniperus procera Hochst. (Text-fig. 36) shows 22 chromosomes in root-tips. Two of these have a subterminal and the rest a median or submedian centromere.

J. rigida and *J. virginiana* have been worked out by Sax & Sax from endosperm. Eleven chromosomes are present, but no morphology is given. Ross & Duncan (1949) worked out *J. virginiana* and *J. horizontalis*; both have $2n = 22$, but only in the latter did they observe a heterobrachial chromosome pair.

Text-fig. 36. *Juniperus procera*, $2n = 22$.

Text-fig. 37. *J. phoenicea*, $n = 11$, metaphase I.

Eleven bivalents have been counted in microspore mother cells of *J. phoenicea* Linn. (Text-fig. 37), *J. bermudiana* Linn., and *J. virginiana* Linn. var. *scopulorum* Jones. Meiosis in all these species is normal.

J. chinensis pfitzeriana (Sax & Sax, 1933) and *J. squamata meyeri* (Jensen & Levan, 1941) are tetraploid. In the former there are 22 bivalents and in the latter there are 44 chromosomes in somatic tissues.

CONCLUSIONS

The total numbers of genera and species of Coniferales are 45 and 447 respectively. These figures have been compiled from Dallimore & Jackson (1948), but with the addition of the monotypic *Metasequoia*, and treating the two species of *Sequoia* as two distinct genera. Hybrids have been excluded. Under the so-called Pinares (Abietaceae, Taxodiaceae, Cupressaceae and Araucariaceae) there fall 35 genera and 335 species. Out of these 27 genera and only 102 species have been cytologically investigated so far. A résumé of all this work, including this study, is given in Table 2. Darlington & Janaki Ammal's *Atlas* (1945), Wang (1948) and Christiansen (1950) have also been consulted in the preparation of this table.

After a careful perusal of Tables 1 and 2 some conclusions emerge.

The chromosome numbers follow taxonomic grouping. In every family a base number can easily be recognized: 12 for the Abietaceae, 11 for the Taxodiaceae and Cupressaceae, and 13 for the Araucariaceae. The families are essentially homoploid. *Pseudotsuga* and *Pseudolarix* in the Abietaceae, and *Sciadopitys* in the Taxodiaceae are the only genera which are not in line with the above statements.

The chromosome number of every genus (except the above mentioned ones) is therefore the base number of the family except in *Sequoia*, where it is its multiple. It remains constant within a genus, or in a few cases it may be a multiple (cf. *Larix* and *Juniperus*). The various genera usually differ in having different karyotypes. However, some genera have the same karyotype. Such a situation is met with in *Picea-Tsuga* (Abietaceae), *Cryptomeria-Cunninghamia*, *Taxodium-Sequoiadendron* (Taxodiaceae), *Actinostrobus-*

Callitris-Tetraclinis-Widdringtonia-Thuja occidentalis var. *compacta* and *Cupressus-Juniperus-Thuja orientalis* (Cupressaceae). In some cases these genera form compact alliances within their respective families. This is particularly true of *Picea* and *Tsuga* in the Abietaceae and *Actinostrobus*, *Callitris* and *Widdringtonia* in the Cupressaceae. In fact, the latter three genera are so close morphologically that Saxton (1910) segregated them in a subfamily Callitroideae.

As stated earlier the karyotype within a genus remains remarkably constant except within the genus *Thuja*. *T. orientalis* and *T. occidentalis* differ in their karyotypes (see Tables 1 and 2). In this connexion it is of interest to note that Buchholz (1929), on the

Table 1. *Summary of observations*

(Sat. = satellite, s.c. = secondary constriction)

Name of species	Chromosome no.	No. of sub-terminal chromo-somes	No. of median or submedian chromosomes	Locality and collector
Pinus canariensis	$2n=24$	—	24 (3 s.c.)	R. N. Khoshoo
P. caribaea	$2n=24$	—	24 (2 s.c.)	R. N. Khoshoo
P. gerardiana	$2n=24$	—	24 (8 s.c.)	Local grocers
P. halepensis	$2n=24$	—	24	R. N. Khoshoo
P. khasya	$2n=24$	—	24 (4 s.c.)	R. N. Khoshoo
P. lambertiana	$2n=24$	—	24 (6 s.c.)	R. N. Khoshoo
P. nigra	$2n=24$	—	24	R. N. Khoshoo
P. pinaster	$2n=24$	—	24	R. N. Khoshoo
P. ponderosa	$2n=24$	—	24	R. N. Khoshoo
P. radiata	$2n=24$	—	24 (4 s.c.)	R. N. Khoshoo
P. roxburghii	$2n=24$	—	24 (6 s.c.)	R. N. Khoshoo
P. wallichiana	$2n=24$	—	24 (6 s.c.)	Bandipore (Kashmir), R. N. Khoshoo
P. merkusii	$n=12$	—	—	F.R.I. (Dehradun), R. N. Khoshoo
Cedrus deodara	$n=12$	1	11 (1 s.c.)	Dalhousie, P. N. Mehra
Picea smithiana	$n=12$	3 (1 s.c.)	9 (2 s.c.)	Tangmarg (Kashmir), R. N. Khoshoo
Abies pindrow	$n=12$	5	7 (2 s.c.)	Tangmarg (Kashmir), R. N. Khoshoo
Cunninghamia lanceolata	$2n=22$	—	22 (2 s.c. and 2 Sat.)	F.R.I., R. N. Khoshoo, Chandra Nursery, Sikkim
Cryptomeria japonica	$2n=22$	—	22	F.R.I., R. N. Khoshoo, Chandra Nursery, Sikkim
Taxodium mucronatum	$2n=22$	2	20 (2 s.c.)	F.R.I., M. B. Raizada
Actinostrobus pyramidalis	$2n=22$	—	22 (2 s.c.)	Forestry Commission of N.S. Wales
Callitris calcarata	$2n=22$	—	22 (2 s.c.)	Forestry Commission of N.S. Wales
C. cupressiformis	$2n=22$	—	22 (2 s.c.)	Forestry Commission of N.S. Wales
C. glauca	$2n=22$	—	22 (2 s.c.)	Forestry Commission of N.S. Wales
C. morrisoni	$2n=22$	—	22 (2 s.c.)	Forestry Commission of N.S. Wales
C. propinqua	$2n=22$	—	22 (2 s.c.)	Forestry Commission of N.S. Wales
C. robusta	$2n=22$	—	22 (2 s.c.)	Forestry Commission of N.S. Wales
C. verrucosa	$2n=22$	—	22 (2 s.c.)	Forestry Commission of N.S. Wales
Widdringtonia cupressoides	$2n=22$	—	22 (2 s.c.)	Chandra Nursery
Tetraclinis articulata	$2n=22$	—	22	F.R.I., T. N. Khoshoo
Thuja orientalis	$n=11$	1	10 (1 s.c. and 1 Sat.)	Local, T. N. Khoshoo
T. occidentalis var. *compacta*	$2n=22$	—	22 (2 s.c.)	Chandra Nursery
Cupressus funebris	$n=11$	1	10 (1 Sat.)	Local, T. N. Khoshoo
C. sempervirens	$2n=22$	2 (2 s.c.)	20	Bandipore, T. N. Khoshoo
C. torulosa	$n=11$	1	10 (1 Sat.)	Dalhousie, P. N. Mehra
C. arizonica	$n=11$	—	—	F.R.I., R. N. Khoshoo
C. cashmeriana	$n=11$	—	—	F.R.I., R. N. Khoshoo
C. lusitanica var. *benthami*	$n=11$	—	—	F.R.I., R. N. Khoshoo
Juniperus procera	$2n=22$	2	20	F.R.I., R. N. Khoshoo
J. bermudiana	$n=11$	—	—	F.R.I., R. N. Khoshoo
J. phoenicea	$n=11$	—	—	F.R.I., R. N. Khoshoo
J. virginiana var. *scopulorum*	$n=11$	—	—	F.R.I., R. N. Khoshoo

basis of embryological evidence, upheld the view of some older taxonomists that *T. orientalis* should be raised to generic rank and be named as *Biota orientalis*.

Excellent examples of constancy of the basic karyotype within a genus are *Pinus*, *Callitris* and *Cupressus*. A similar situation exists in Cycads (Sax & Beal, 1934) and in the genus *Ephedra* (Mehra, 1946).

Table 2. *Résumé of cytological work on Abietaceae, Taxodiaceae, Cupressaceae and Araucariaceae*

Name of genus	Total no. of species	No. of species worked out	Haploid chromosome number	No. of terminal chromosomes	No. of subterminal chromosomes	No. of median and submedian chromosomes
ABIETACEAE:						
Pinus	73	31 {24	12	—	—	12
		7*	12	—	—	—
Picea	29	6 {3	12	—	3	9
		3*	12	—	—	—
Abies	42	6 {3	12	—	5	7
		3*	12	—	—	—
Keteleeria	2	1*	12	—	—	—
Pseudotsuga	6	1	13	1	6	6
Tsuga	11	3 {2	12	—	3	9
		1*	12	—	—	—
Cedrus	4	2	12	—	1	11
Larix	11	8 {1	12	—	6	6
		1	12	—	6	6
		—	24	—	12	12
		6*	12	—	—	—
Pseudolarix	1	1	22	— 20†	—	2
TAXODIACEAE:						
Sciadopitys	1	1*	10	—	—	—
Cryptomeria	1	1	11	—	—	11
Cunninghamia	2	1	11	—	—	11
Taiwania	1	1*	11	—	—	—
Taxodium	3	2 {1	11	—	1	10
		1*	11	—	—	—
Sequoia	1	1*	33	—	—	—
Sequoiadendron	1	1	11	—	1	10
Metasequoia	1	1*	11	—	—	—
Unworked genera: *Athrotaxis* and *Glyptostrobus*						
CUPRESSACEAE:						
Juniperus	49	9 {1	11	—	1	10
		6*	11	—	—	—
		2*	22	—	—	—
Callitris	19	7	11	—	—	11
Tetraclinis	1	1	11	—	—	11
Widdringtonia	5	1	11	—	—	11
Actinostrobus	2	1	11	—	—	11
Cupressus	12	6 {3	11	—	1	10
		3*	11	—	—	—
Chamaecyparis	6	1*	11	—	—	—
Thuja	6	4 {1	11	—	1	10
		1	11	—	—	11
		2*	11	—	—	—
Unworked genera: *Callitropsis, Diselma, Fitzroya, Fokienia, Libocedrus,* and *Thujopsis*						
ARAUCARIACEAE:						
Agathis	15	1	13	4	—	9
Araucaria	10	3 {1	13	4	—	9
		2*	13	—	—	—

* Species in which either the meiotic number is known or detailed morphology of the chromosomes is not reported. † Sax & Sax (1933) have not clearly mentioned to which category the chromosomes belong.

The specific differences are to be correlated with differences in detail, such as number and nature of secondary constrictions and satellites. This is true of *Pinus* and *Cupressus*. On the other hand, the present evidence shows constancy even in these characteristics within the genus *Callitris*.

If it is correct that 12 is the base number of the Coniferales, which, indeed, is also represented in such an ancient group as the Ginkgoales, then the basis of cytological evolution has been loss or gain of a chromosome at the family level. This has been coupled with structural rearrangements and mutations, which factors seem to be responsible for evolution at generic level.

The loss of a chromosome has been responsible for the evolution of the Taxodiaceae and Cupressaceae. This involves a loss of a centromere which follows translocation of all the essential genes to the rest of the chromosomes of the complement. This was suggested by Sax & Sax (1933), and this mechanism has been experimentally demonstrated, though in an Angiosperm—*Crepis*—by Tobgy (1943).

Cases of gain of a chromosome are not many: *Pseudotsuga* (Abietaceae) and the family Araucariaceae. This always involves duplication of a centromere, and could be achieved by a system of translocations as proposed by Darlington (1937).

That structural rearrangement has played an important role in differentiation of genera is clear from the karyotypes of the genera of Abietaceae.

At the species level evolution seems to be chiefly at a submicroscopic level involving gene mutations. This is why there are increasingly numerous reports of both natural and artificial hybrids in conifers. Perhaps the main checks to hybridization are physical isolation and time of flowering of the various species of a genus.

Polyploidy has played an insignificant role in the evolution of conifer families, genera and species. The increase in the chromosome number in *Pseudolarix* does not represent a doubling either in quality or in quantity. It is of interest to note that the present data indicate that polyploidy is lacking in cycads, but in the genus *Ephedra* there are many polyploid species reported (Florin, 1932; Resende, 1937; Mehra, 1946; Hunziker, 1953; Fuchs, 1954).

SUMMARY

The paper deals with a cytological study of forty-one conifer species belonging to fourteen genera and distributed within the Abietaceae, Taxodiaceae and Cupressaceae. Observations have been made from the squashes of female gametophytes, stem apices, root-tips, young leaves and pollen mother cells. The cytological details of all these species are summarized in Table 1.

Families and genera are essentially homoploid. A basic karyotype is characteristic of almost every genus. Species within a genus either differ in the number and nature of secondary constriction and satellites (*Pinus* and *Cupressus*) or resemble one another even in these details (*Callitris*). Various genera differ in chromosome morphology, but in every family some of the genera have essentially the same karyotype. The mechanisms of evolution have been gain or loss of a chromosome, structural rearrangements, and gene mutations. Polyploidy has played but little role.

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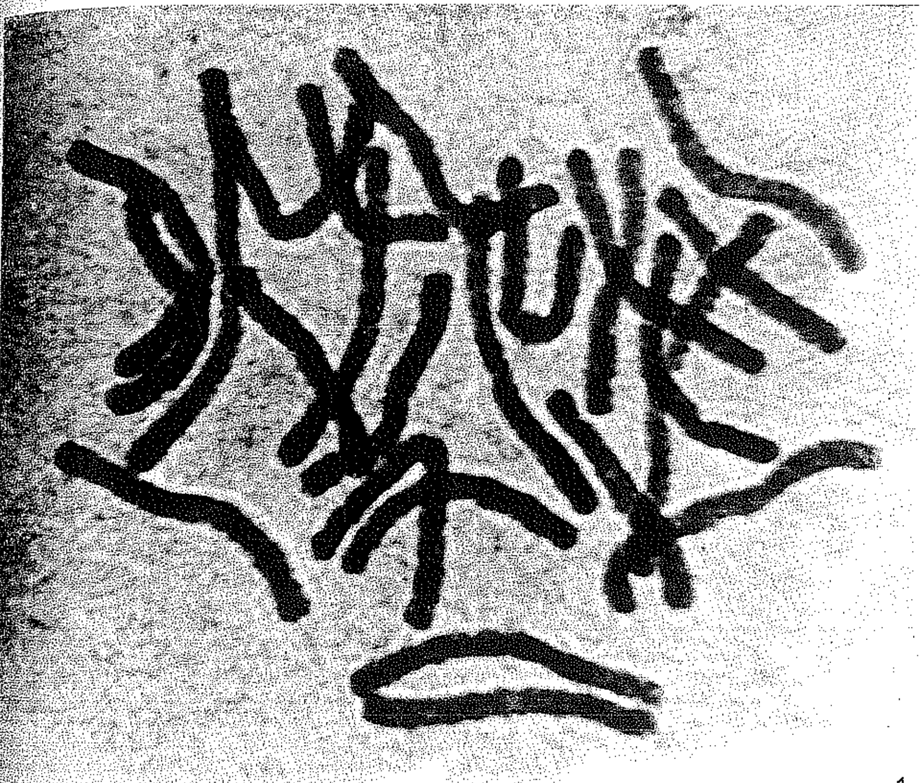
EXPLANATION OF PLATE

Fig. 1. *Pinus gerardiana*, $2n = 24$. × 1700. Same as Text-fig. 3.
Fig. 2. *Callitris calcarata*, $2n = 22$. × 1700. Same as Text-fig. 21.
Fig. 3. *Callitris robusta*, $2n = 22$. × 1700. Same as Text-fig. 26.



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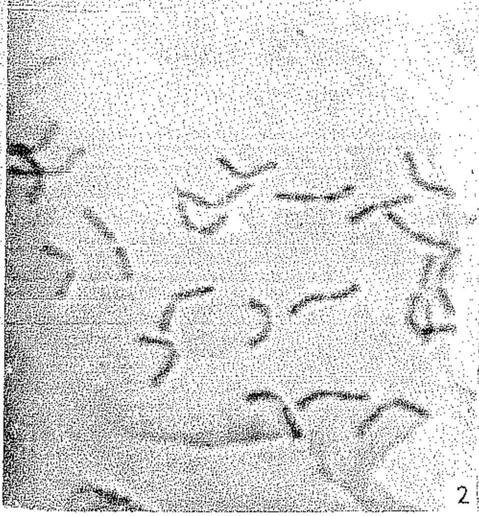

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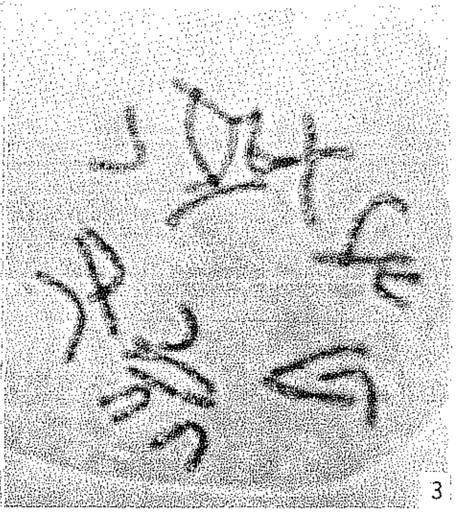

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