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# Karyotype Analysis of the Genus Pinus – Subgenus Strobus¹)

By L. C. SAYLOR<sup>2</sup>)

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#### Summary

Descriptions of karyotypes (based primarily on centromere location and arm lengths) are presented for 22 pine species of the subgenus *Strobus* (soft pines). This study concludes a comprehensive investigation of the genus *Pinus* for which karyological information now has been presented for 87 species.

Results for this group of soft pines are similar to those obtained in previous studies. The karyotypes show a remarkable degree of similarity based on general features, yet they are not always identical. Again the karyological data support in general other taxonomic evidence of species relationships, and they indicate the genus has been quite conservative in changing major features of its karyotype.

Important karyological features of the subsections are described and compared.

Key words: Karyotype analysis for 22 pine species of subgenus Strobus.

## Zusammenfassung

Für 22 Kiefernarten der Sektion Strobus werden die Karyotypen erstmalig aufgrund der Lage der Centromeren sowie der Chromosomenschenkellängen beschrieben. Diese Studie schließt eine eingehende Untersuchung ab, aus der nunmehr karyotypische Informationen für insgesamt 87 Arten der Gattung Pinus vorliegen. Die Ergebnisse für die Sektion Strobus sind denen ähnlich, die in früheren Untersuchungen erzielt wurden. Die Karyotypen zeigen einen bemerkenswerten Grad an Ähnlichkeiten bei den Hauptmerkmalen, sie sind aber nicht immer identisch. Wiederum unterstützen die karyotypischen Daten im allgemeinen andere taxonomische Merkmale der Verwandtschaft zwischen den Arten und zeigen an, daß die Gattung bei der Änderung von Hauptmerkmalen der Karyotypen sehr konservativ gewesen ist. Wichtige Karyotypmerkmale der Untersektionen werden beschrieben und verglichen.

#### Introduction

Although previous studies have shown that the karyotypes of pine species are in general similar, differences have been observed that are useful in understanding relationships among some of the species. Based primarily on centromere location, Saylor (1964, 1972) found differences between certain subsections of hard pines (subgenus *Pinus*) and occasionally between species. Pederick (1967, 1970) also illustrated interspecific differences in his detailed karyotypic analyses based on the size and location of secondary constrictions.

Karyotypes are described in this paper for 22 species of soft pines (subgenus Strobus)³). This report includes data for a majority of the species in this subgenus, and concludes the comprehensive karyological study of the genus Pinus on which 87 species have now been reported.

# **Materials and Methods**

Karyotype data for this and previous studies were obtained by using identical procedures. Slides were prepared from squash preparations of root-tip meristerms of 2—12 month old seedlings. The root-tips were pretreated in oxyquinoline (0.3 g/l.) for 24—36 hours at 12° C, fixed in 3:1 ethyl alcohol-acetic acid for 1—4 hours, hydrolyzed in 1N HCl for 10—15 minutes at 60° C, and stained in acetocarmine.

Chromosome dimensions were obtained from projection drawings as described by Saylor (1961). To allow comparisons, the data are presented in the same manner used in previous reports. For each karyotype, the chromosomes are arranged from 1—12 according to a descending order of lengths of the short (a) arms. (Chromosomes with median and submedian centromeres are defined by short-arm/long-arm ratios of 0.75—1.00 and 0.50—0.75, respectively.)

The diagnostic features used in making species comparisons included:

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Professor of Genetics and Forestry, School of Forest Resources, North Carolina State University, Raleigh, North Carolina 27650.

<sup>3)</sup> The taxonomic classification used in this presentation follows that of Critchfield et al. (1966) and Little et al. (1969).

- (1) Patterns caused by divergence of the long (b) arm lengths from a descending order comparable to that for the short (a) arms. (See Table 1, P. koraiensis chromosomes 5, 7, 9, 11.)
- (2) Location in the sequence of chromosomes with the largest or smallest short arm/long arm ratios (other than chromosome 12).
- (3) Places where the greatest differences in the lengths of the short (a) arms occur between adjacent chromosomes other than between chromosomes 11 and 12 whose a arms are always the most different. (See

Table 1. - Mean arm lengths in millimeters of chromosomes magnified 2000X. (Horizontal lines denote b arm lengths that break descending sequence of values — See text, Vertical lines denote location of greatest difference in a arm lengths between adjacent chromosomes other than between chromosomes 11 and 12 - See text. x, \*, and z denote secondary constrictions in the distal, medial, and proximal portion of the arms, respectively.)

P. koraiensis

P. pumila

15.6 .930 14.7\* .946

P. sibirica

14.2 13.6

15.4 .922 14.5 .938

5 6 7 8 9 10 11	12.8	12.9 13.4 963 12.7 14.7 .864 12.4 13.0 .954 12.2 14.1 .865 11.7* 13.0 .900 11.0 12.1 .909 9.5 12.8 .742 8.0 10.9 .734	12.9	periods, or differential reaction of the chromosomes to the pretreatment, or a combination of the two.  Although the location of secondary constrictions is included in the karyotype descriptions, the reliability must be considered marginal (as reported previously — Saylor 1961 and 1964) because these constrictions often do not					
	P. cembra	P. albicaulis	P. strobus		,	using the above			
1 2 3 4 5 6 7 8 9 10 11	16.0   17.7   .904     15.4   15.7   .981     15.0   15.4*   .974     14.7   16.4   .896     14.4   15.3   .941     13.9   15.8   .880     13.5   14.4   .938     13.2   13.7   .964     12.7   13.5   .941     11.4   14.3   .797     9.3   13.3   .699	14.6 16.2 .901 14.2 15.3 .928 13.7 14.7 .932 13.4 14.0 .957 13.1 13.7 .956 12.6 15.2 .828 12.3 13.2 .932 11.9 12.8 .930 11.7 13.7* .854 11.2 11.8 .949 10.7 13.5 .792 8.7 12.6 .690	15.0 16.1 .932 14.3 15.2 .941 13.9* 14.6 .952 13.6 13.9* .978 13.3 <u>15.1</u> .881 13.1* 14.2 .922 12.7 13.3 .955 12.3 <u>14.1</u> .872 12.0* 12.8 .937 11.5 12.7 .906 10.9 <u>13.4</u> .813 8.6 12.0 .717	able variation existed in the detection of secondary constrictions among the various species. Those cases in which they were especially easy to determine are noted later in the discussion; for those listed only in the tables, they					
Chromo- some	Arms a/b	Arms a/b	Arms a/b	Chromo- some	Arms a/	b Arms	a/b Arms	a/b	
	a b	a b	a b		a b	a b	a	b	
1 2 3 4	P. monticola  15.9	P. lambertiana 15.8 17.0 .929 15.3* 16.2 .944 14.7* 15.6 .942 14.4 14.7 .980	P. flexilis 14.1 15.1 .934 13.2 13.6* .971 12.9 14.8 .872 12.7 13.0 .977	1 2 3 4 5	P. cembroides 15.1 15.7 .96 14.6 15.2 .96 14.0 14.5* .96 13.5 13.9 .97 13.2 14.9 .88	15.4 16.2 15.0 15.7 1 14.7 15.5	.982 .951 .955 .955 .948 13.4	15.6 .962 14.6 .959 15.5* .884 13.8 .971 15.0* .873	
5 6 7 8 9 10	14.4* 15.8 .911 14.0 14.6* .959 13.8* 15.4 .896 13.6 13.8 .986 13.0 14.5 .897 12.4 13.7 .905 11.4 14.0 .814	14.1 15.7 .898 13.9 14.7 .946 13.6 15.3 .889 13.2 14.1 .936 12.9 15.2 .849 12.1 13.2 .917 11.5 14.1* .816	12.5 13.6 .919 12.2 13.0 .939 12.0 12.6 .952 11.7 14.4 .812 11.2 13.5 .830 10.9* 11.8 .924 9.8 12.1 .810	6 7 8 9 10	13.0 13.7 .94 12.8 13.4 .96 12.4 14.8* .83 12.0 13.3 .90  11.4 12.6 .90 9.6 11.8 .81	99 14.0 15.2 33 13.8 14.6 88 13.4 15.3* 12 12.8 14.5 5 12.0 13.5 4 10.6 12.6	.921 12.9 .945 12.5 .876 12.2 .883 12.0 .889 11.4	13.0 .962 14.4 .847 13.1 .916 12.8 .891 11.8* .856	
12	9.1 13.0 .700	8.8 13.8 .638	8.4 11.6 .724	12	7.9 <u>12.5</u> .63  P. gerardiana	2 8.5 <u>13.7</u> P. bungea		12.4 .702	
1 2 3 4 5 6 7 8 9 10 11	P. strobiformis  15.2 15.9 .956  14.7 17.0 .865  14.4 15.6 .923  14.1 14.7 .959  13.8 15.6* .885  13.6 14.4 .944  13.4 14.0 .957  13.1 14.9 .879  12.6 14.1 .894  12.0* 13.1 .916  11.1* 13.4 .828  8.9 12.8 .695	P. syacabutte   14.4   15.8   914   13.7   14.5   945   13.2   13.7   964   12.8*   13.2*   970   12.6   14.7   857   12.4   13.9   957   11.7   12.9   907   11.3   12.4   911   10.8   13.0   831   19.9*   11.5   687	P. peuce    15.4   16.3   .945     14.8   15.1   .980     14.4*   15.6   .923     14.1   14.6   .966     13.8   14.2   .972     13.6   15.0*   .997     13.2   13.6   .971     12.8   13.4   .955     12.6   14.0   .900     12.2   13.1   .931     11.5   13.8   .833     9.0   12.9   .698	1 2 3 4 5 6 7 8 9 10 11 12	16.7 17.5 .95 15.8 16.6 .95 15.4 15.7 .98 15.0 16.8 .89 14.6 15.5 .94 14.0 15.5 .94 13.2 13.9 .95 13.6 14.2 .95 13.6 15.2 .82 11.9 13.2 .82 11.9 13.2 .82 11.9 13.2 .82 11.9 13.2 .82	4   15.8   16.4   14.8   15.5   14.4   14.6   3   14.9   13.5   14.6   3   14.0   15.7*   2   13.8   14.9   13.5   14.6   7   13.2   13.9   0   12.9   15.4   9   12.5   13.5   12.1   12.9   2   11.0   14.5   2   11.0   14.5	.963 15.0 .955 14.6 .986 14.2 .092 13.6 .913 13.4 .925 13.2 .950 13.0 .838 12.6 .926 12.2 .938 11.4 .759 10.5	16.3 . 920 15.5* . 942 14.8 . 959 14.4 . 944 15.4 . 870 13.8 . 956 14.6 . 890 13.4 . 940 14.2* . 859 12.6 . 905 13.5 . 778 13.5 . 633	
1 2 3 4 5 6 7 8 9 10 11	P. armand11  15.2 16.2 .938  14.5 15.1* .960  14.0 14.7 .952  13.7 14.2 .965  13.4 15.8 .848  13.0 13.9 .935  12.7 14.9 .852  12.5 13.5 .926  12.2* 13.0 .938  11.8 14.0 .843  10.9 12.3 .886  8.8 12.1 .727	P. griffithii  14.4 15.0 .960  13.5 14.3 .944  13.1 13.8 .949  12.7 13.3 .955  12.5 12.7 .984  12.2 14.0 .871  11.9 12.5 .952  11.6 13.4 .866  11.4 12.1 .942  10.9 12.8 .852  7.8 11.6* .672	P. parviflora  14.8 15.5 .955  14.1 16.2* .870  13.8 14.6 .945  13.5* 14.3 .944  13.2 13.9 .950  12.9 14.8 .872  12.7 13.1 .969  12.3 14.1 .872  12.0 12.7 .945  11.5 12.2 .943  10.9 13.3 .820  8.6 12.0 .717	1 2 3 4 5 6 7 8 9 10 11	P. aristata µ14.3 15.1 .94 13.7 14.2 .96 13.2 13.7 .96 12.9 14.2 .90 12.7 13.2* .96 12.2 14.4 .84 11.8 12.6 .93 11.5 12.2 .94 µ11.3 13.2 .85 10.4* 11.5 .90 10.0 12.2 .82 7.4 11.8 .62	5 3 8 2 2 7 6 6 3 6 6 4 4 0			

Table 1, difference in a arm lengths between chromosomes 1—2 and 10—11 for P. koraiensis.)

(4) Locations of primary and secondary constrictions.

It is recognized that this method of evaluation is subject to criticism because of the similarity in a arm lengths of chromosomes in adjacent positions (especially those of intermediate size: e.g. numbers 3-8) and the resulting opportunity for reversals in the order of the chromosomes. This problem has been described by MATERN et al. (1968) and should be kept in mind in all analyses of the data. The karyotype patterns presented here are simply the best interpretation of the data from a sample judged adequate according to the agreement of data from different seedlings. The patterns described were present in more than 50 percent of the plates obtained for a given species, and they were obtained easily by minor adjustments for most of the other plates. Only the karyotype features particularly characteristic of the subsection (and on occasion for individual species or groups of related species) are discussed in any detail.

The values in Table 1 are mean arm lengths, and do not provide critical information about interspecific differences in chromosome lengths. The apparent differences between species are most likely the result of unequal pretreatment

Table 2. — Diagnostic features of species karyotypes obtained by arranging the chromosomes in a descending order of the a (shorter) arm length. (See Table 1).

Species	Number of Plates	Number of	"b" Arm Sequence Chromosomes showing exception to a descending	Short/Long Arm Ratios Chromosomes with	
	Drawn	plants	order in b (longer) arm lengths	Largest	Smallest1/
Subsection Cembrae			_	Ü	
P. koraiensis Sieb. & Zucc.	17	8	5, 7, 9, 11	4, 3	11, 9
P. pumila Regel	24	11	6, 8, 11	5, 7	11, 6
P. sibirica Du Tour	10	3	3, 5, 7, 9, 11	4, 6	11, 9
P. cembra L.	15	5	4, 7, 11	2, 3	11, 7
P. albicaulis Engelm.	19	11	6, 9, 11	4, 5	11, 6
Subsection Strobi					
P. strobus L.	18	6	5, 8, 11	4, 7	11, 8
P. monticola Dougl.	34	8	5, 7, 9, 11	8, 4	11, 7
P. lambertiana Dougl.	29	13	5, 7, 9, 11	4, 6	11, 9
P. flexilis James	20	11	3, 5, 8, 11	4. 2	11, 8
P. strobiformis Engelm.	25	12	2, 5, 8, 11	4, 7	11, 2
P. ayacahuite Enrenb.	22	13	5, 7, 10	4, 6	11, 10
P. peuce Griseb.	15	5	3, 6, 9, 11	2, 5	11, 9
P. armandii Franch.	20	11	5, 7, 10	4, 2	10, 5
P. griffithii McClelland	15	7	6, 8, 10	5, 1	11, 10
P. parviflora Sieb. & Zucc.	18	8	2, 6, 8, 11	7, 1	11, 2
Subsection Cembroides					
P. cembroides Zucc.	15	4	5 0 10		
P. edulis Engelm.	30	10	5, 8, 12	4, 3	11, 8
P. monophylla Torr & Frem	20	8	5, 8, 12	1, 3	11, 8
monophyrra forr a riem	20	•	3, 5, 8, 12	4, 1	8, 11
Subsection Gerardianae					
P. gerardiana Wall.	14	8	4, 9, 11		
P. bungeana Zucc.	14	7	4, 8, 11	3, 7 3, 1	11, 9 11, 8
			. ,	-, -	, -
Subsection Balfourianae					
P. balfouriana Grev. & Balf.	17	8	5, 7, 9, 11	3, 6	11, 9
P. aristata Engelm.	26	14	4, 6, 9, 11	2, 3	11, 6

 $\underline{1}$ / Not including chromosome number 12

were apparent in approximately half the plates and thus are considered to be at least probable locations of major secondary constrictions. It was never possible in the analysis of these diploid root-tip figures to use location of secondary constrictions with the reliability and precision utilized by Pederic (1967 and 1970) in studying the haploid female gametophyte chromosomes.

## Results and Discussion

Similar to previous studies, the karyotypes of the 22 species included in this report were in general agreement with the basic karyotype described originally by Sax et al. (1933) for the genus. All species had a haploid complement of 12 chromosomes, and except for the smallest chromosome which was always heterobrachial and noticeably different in size, the other 11 chromosomes possessed median centromeres and were rather similar in total length.

Although once again major differences in chromosome number and morphology were not observed, minor differences or special features were detected for some species (*Table 1*—2). Those considered to be significant are discussed below along with the karyotypic features considered to be most characteristic of the subsections.

For the subgenus *Strobus*, there was in general less similarity of karyotypic features for species of the same subsection (or closely related species within a subsection) than occurred in the subgenus *Pinus*. Reasons for this are not clear, but it should be noted that more difficulty was experienced in pairing homologous chromosomes with some species of the subgenus *Strobus* than occurred in the subgenus *Pinus*. Although it was felt this situation did not seriously effect the results, it is considered important enough to report and should be kept in mind in interpreting these data.

## Cembrae

Of the five species in this subsection, four are found in Eurasia and one in North America. The range of *P. pumila* 

overlaps those of both *P. koraiensis* and *P. sibirica*, but *P. cembra* is separated from these species by 2415 km. *Pinus albicaulis* is the lone North American species.

No basic karyotypic pattern of *b* arm sequences exists for this group (*Table 1*). However, the *b* arm of chromosome 11 breaks the descending sequence for all five species. This feature of chromosome 11 is also common in the other subsections of *Strobus* except for the species of *Cembroides*. It occurs much less frequently, however, for species of the subgenus *Pinus*. Another interesting feature of chromosome 11 for this subsection (especially *P. pumila*) is that the centromere tends to be located in a more nearly median location than for the other subsections (except *Gerardianae*).

Although *P. pumila* has generally been considered a variant of the *P. cembra* — *P. sibirica* group, some investigators consider it more closely related to *P. parviflora* (Critchfield *et al.*, 1966). Interestingly, the *b.* arm pattern for *P. pumila* (Figure 1b) resembles that of *P. parviflora* much more than it does *P. cembra* (Figure 1a) or *P. sibirica*.

The b arm of chromosome 3 for P. sibirica was the longest of the complement which is rather unusual. Only two other species of Strobus (and six in the entire genus) have a chromosome other than number 1 with the longest b arm.

## Strobi

More species (14) are grouped in this subsection than in any other in the subgenus *Strobus*. Their location is about evenly divided between Eurasia and North America.

The karyotypes of the 10 species studied were quite variable and no basic or common karyotype could be determined for the subsection or groups of closely related species within it. For the b arm patterns, chromosomes 5, 8, and 11 broke the descending sequence most frequently and could represent the basic pattern from which others evolved. As with all other species of pine in this and previous studies, the most median chromosomes were found

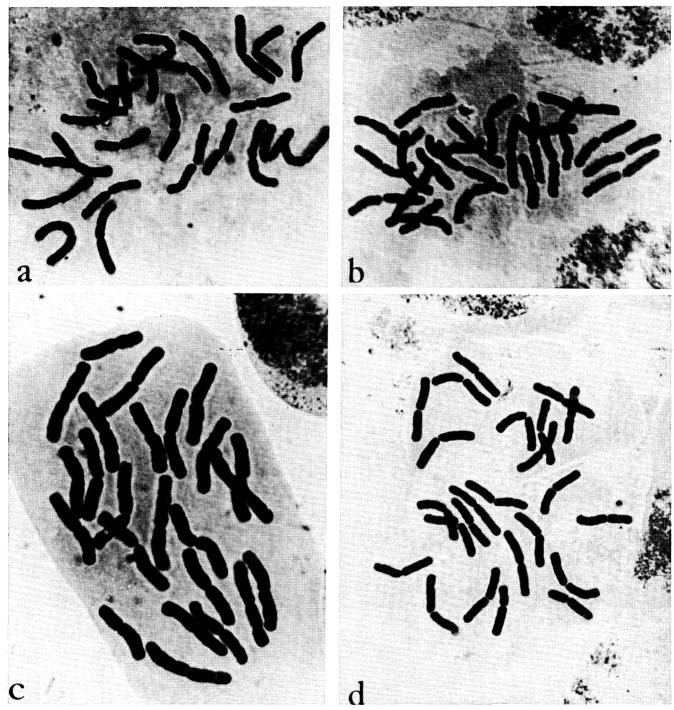


Figure 1. — Metaphase chromosomes from aceto-carmine preparations of root-tip meristems (2n = 24). (a) P. cembra (1050X), (b) P. pumila (1050X), (c) P. flexilis (1150X) (d) P. strobiformis (1350X).

in positions 1-4 while the most submedian were in positions 9-12.

The degree of similarity of karyotypes among related species varied considerably. For example, *P. strobiformis* is known to form a link geographically and morphologically between *P. flexilis* and *P. ayacahuite*, but the karyotypes are not all alike. Although those for *P. flexilis* (Figure 1c) and *P. strobiformis* (Figure 1d) are rather similar, the karyotype of *P. ayacahuite* differs noticeably from the other two. Also, while there was some agreement between *P. strobus* and *P. monticola*, there were few karyotypic features in common between *P. peuce* and *P. griffithii*, two morphologically similar species.

Three species had karyotypes with somewhat special features. *Pinus parviflora* and *P. strobiformis* were the other species of soft pine to have a chromosome other than number 1 with the longest *b* arm; for both species it was number 2. For *P. ayacahuite* (*Figure 2a*), the secondary constriction in the *a* arm of chromosome 11 was the easiest to recognize of any species in the subgenus; it occurred in nearly every plate observed.

# Cembroides

Of the eight pines of this subsection covering parts of southwestern United States and Mexico, only three were

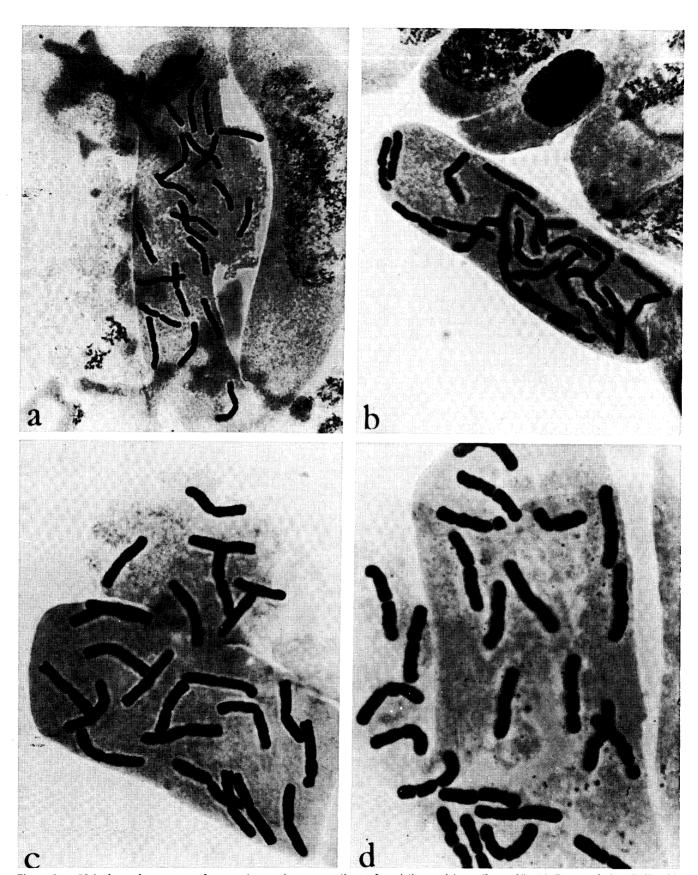


Figure 2. — Metaphase chromosomes from aceto-carmine preparations of root-tip meristems (2n = 24). (a) P. ayacahuite (920X), (b) P. cembroides (1050X), (c) P. gerardiana (1225X), (d) P. aristata (1350X).

studied because of problems in obtaining viable seeds of the others. However, it was easier to determine the karyotypes of those studies--*P. cembroides* (Figure 2b), *P. edu*- lis, and  $P.\ monophylla--and$  there was closer agreement of features among these species than for any other group studied in the subgenus Strobus.

A basic *b* arm sequence of 5, 8, 12 was found for all three; only *P. monophylla* deviated slightly by having the *b* arm of chromosome 3 also break the sequence. Similarly, all three had chromosomes with the most median centromere located in position 1, 3, and 4. A particularly unique feature about the karyotypes of these species involved chromosome 12. The *b* arm of this chromosome broke the descending sequence rather than chromosome 11 which normally is involved. A *b* arm sequence involving chromosome12 did not occur for any other species of soft pine, and it occurred for only three species of hard pines (*P. hartwegii*, *P. rudis*, *P. pringlei*) all of which are found in Mexico.

#### Gerardianae

The karyotypes of the two species of this subsection (*P. gerardiana* and *P. bungeana*) were somewhat similar. Two of the three positions breaking the *b* arm descending sequence are similar in both species. In addition, the centromere of chromosome 11 for both is located in nearly a submedian position. The occurrence of secondary constrictions was quite different, however. So few were observed for *P. gerardiana* (*Figure 2c*) that none were recorded for the karyotype, but for *P. bungeana* they occurred consistently and clearly for chromosome 4 and also chromosome 12 which is very unusual.

#### Balfourianae

The two species of this subsection (P. balfouriana and P. aristata) had only minimal agreement in karyotypes. Two positions (9 and 11) out of four breaking the b arm sequence were similar for both species; for the location of the most median or submedian chromosomes they agreed for one position each, number 3 and 11 respectively.

Although the location of secondary constrictions did not agree, the constrictions were very easy to determine, especially the one found in the a arm of chromosome 10 for P. aristata (Figure 2d).

## **Conclusions**

The data from this concluding study along with those reported on previously (Saylor 1964, 1972) constitute the most comprehensive body of karyological information ever presented for the genus *Pinus*. When evaluated collectively they cover 87 species and provide an important overview of general karyological features of the genus.

It may be concluded from these results that indeed as reported by earlier investigators (e.g. Sax et al. 1933) the karyotypes of all species of pine have a remarkable degree of similarity based on general features of chromosome number, length, and centromere location. Thus it would appear that his genus, which has been in existence for millions of years and been subjected to a wide variety of

selection forces, has been quite conservative in changing major features of its karyotype. Polyploidy or even the addition or loss of a single chromosome does not exist in the genus at any level except for an occasional individual. Similarly, evolution has proceeded with quite limited involvement of chromosome translocations and inversions that include the centromere. Although it was anticipated initially that more differences would be found, it is nevertheless important to describe the basic species karyotypes and to document the similarities as well as the differences that do exist.

Careful evaluation of the data did indicate that although the karyotypes are basically similar they are not always identical. Even with the constraints listed in the methods section, it was felt that the techniques were reliable enough to provide evidence of occasional differences between subsections, groups of related species within subsections and even among individual species. Examples from this and other studies include: (1) The subsection *Sylvestres* which is delimited by the heterobrachial chromosome 11. (2) The six species (three soft pines and three hard pines) which have a unique feature involving chromosome 12. (3) Six individual species (found in five different subsections) that have the unusual condition of a chromosome other than number one with the longest *b* arm.

Karyotype studies along with those from meiotic analyses (e.g. Saylor et al. 1966) indicate that structural changes of various types have occurred in pine chromosomes. In some instances the changes are great enough and of a type that can be combined with other descriptive data for a better understanding of taxonomic relationships. The results of this and previous karyological studies (Saylor 1964, 1972) have in general supported findings using other characteristics. They have not provided evidence to contradict major taxonomic relationships established previously.

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