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A STUDY OF PINUS SUBSECTION CEMBROIDES I:
The single-needle Pinyons of the Californias and the Great Basin

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ABSTRACT. The pinyons or nut pines (Pinaceae), *Pinus* subsect. *Cembroides* Engelm., occur only in the western United States and Mexico. Among them the needle number per fascicle ranges from 1 to 5. This study reports the results of an extensive investigation by means of populational samples of the pinyons with single-needle fascicles whose natural ranges lie mainly in the Californias and the Great Basin, but with minor extensions into Colorado River drainages in Nevada and Arizona. Three taxa with limited sympatry are recognized, mapped and described. *Pinus monophylla* Torr. & Frém. is retained, but with a restricted range. *Pinus californiarum* D. K. Bailey is proposed to segregate the single-needle pinyons of the desert mountains of southern California and northern Baja California. These trees are demonstrated to have, at best, a rather limited connection with *P. monophylla*. Lastly *Pinus edulis* Engelm. var. *fallax* Little, which barely enters the investigated region, is demonstrated to be more closely allied to *P. californiarum* than to either *P. monophylla* or *P. edulis*; it is therefore transferred as *P. californiarum* subsp. *fallax* (Little) D. K. Bailey. Detailed evidence is presented to justify these proposals. Speculative generalizations, supported by limited direct evidence, are made relating present and past distributions. Finally an hypothesis is advanced to explain the origin and apparent stability of *P. californiarum* subsp. *fallax*.

INTRODUCTION

Studies of the biosystematics of conifers are difficult because of their natural plasticity, a paucity of good characters and the failure of collectors generally to sample enough trees in local populations to permit accurate generalizations. With these considerations in mind the present study may be viewed in a wider context. Thus the geographic area included is one of the few parts of the world where conifers, and *Pinus* in particular, are actively evolving and have speciated in response to local and sometimes extreme environmental conditions and where their distributions reflect the climatic pressures resulting from the glacial advances and retreats during the Pleistocene. This area is, however, an element of a much larger area, including most of the southwestern United States, mainland Mexico, and extending into Central America. In the present work the populations studied, though spread over a substantial area (see Fig. 1), are accessible enough to be closely investigated and their morphological details elucidated at a populational level. The area is also in a relatively unspoiled condition and, except for some localities at the western edges of the deserts of southern California, not greatly damaged by human activities. Extensive studies of *Juniperus* in the larger area by Zanoni & Adams (1975) have also disclosed evidence of such active evolution. Other similar actively evolving coniferous complexes probably exist in areas such as the Sino-Himalayan region (C. N. Page, pers. comm. 1986).

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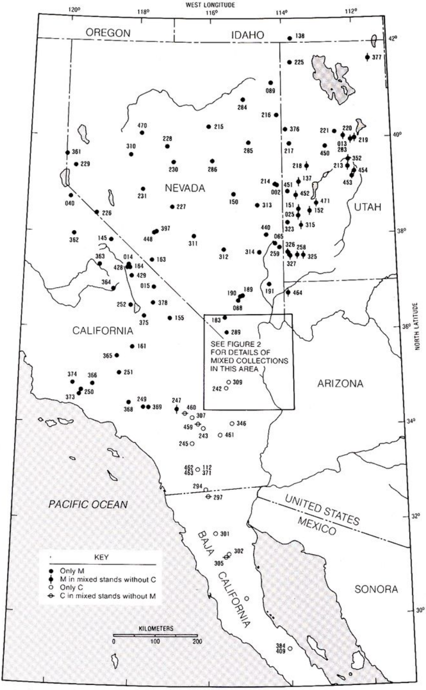

FIG. 1. Geographical distribution of the collections of *Pinus monophylla* (M) and *P. californiarum* (C) in pure and mixed stands, with collection numbers. See Appendix for full details of each collection, except for the isolated collection without a number in Baja California. Specimens from that locality, Cerro Matomí, have been seen only in herbaria. Collections 470 (north central Nevada) and 471 (SW Utah), were made too late for inclusion in the appendix and further use.

THE PRESENT POSITION

The single-needle pinyons of the Great Basin have been known to botanists since the report of Frémont's collection in 1844. In the subsequent report (Frémont, 1845, p. 319 and plate 4) it received the name *Pinus monophylla* (as *monophyllus*) Torr. & Frém. and became the first pinyon to be described formally from territory that is now in the United States. Because of its single-needle fascicles it was then, and for some time thereafter, regarded as a curiosity and dismissed by some botanists (Sargent, 1897, p. 51, footnote 2) as merely a western form with connate needles of the 2-needle pinyon, *Pinus edulis* Engelm. At the beginning of the 20th century Voss (1907, p. 95) went further and subordinated all the pinyons of the United States, including *Pinus quadrifolia* Parl., to the status of varieties of *Pinus cembroides* Zucc. (as *cembrodes*). If *Pinus culminicola* Andresen & Beaman of northern Mexico had been known in 1907, it would surely have been subordinated similarly. Shaw (1909, 1914) accepted Voss' lead. However most American botanists since Shaw have preferred, for many reasons including convenience, to retain *P. monophylla*, *P. edulis* and *P. quadrifolia* as distinct species. Thus all single-needle pinyons were taken, uncritically, to be *P. monophylla*.

This view was first challenged by Torrey (1860) and later by Tidestrom & Kittell (1941) in two different taxonomic proposals for the single-needle pinyons of Arizona. Both proposals are *nomina nuda* according to Articles 34.1 and 36.1 respectively of the ICBN. For this reason, Little (1968, p. 371), considering the close geographical association with *P. edulis*, including evidence of natural hybridization, proposed the name *Pinus edulis* var. *fallax* Little. However, reservations have existed in the minds of some botanists familiar with the Arizona single-needle pinyon as to Little's proposal, though most would accept the idea of independent taxonomic status. Lanner (1974, p. 108), however, in a study of natural hybridization between *P. edulis* and *P. monophylla*, notwithstanding Little's var. *fallax*, chose to retain the Arizona single-needle pinyon in *P. monophylla*. The rationale for this choice was first expressed in a slightly earlier publication (Lanner & Van Devender, 1974, p. 208) which states that 'it is simpler to regard the monophylly mutation as having occurred once rather than twice.' Thereby, it was presumed that a single taxon arose. The statement represented an hypothesis and did not constitute a demonstrated fact. It has not reduced confusion but, as will be shown, has perpetuated it. Sudworth (1917) provided two illustrations (plates 13 and 14) labelled *P. monophylla*, differing markedly in needle thickness, but offered no explanation. Perhaps Roof (1978), in what may be termed a diatribe, expressed best and most picturesquely the frustration which he and others have felt concerning the taxonomic status of the single-needle pinyons and their relationship with *P. edulis*. The taxonomic proposals which follow will doubtless be regarded with disfavour by conservative taxonomists. They are nevertheless made in the interests of deeper understanding and to reduce, and perhaps eliminate, some of the inaccuracies, confusion and equivocation that so irritated Roof. The proposals are based on significant differences among large populations and in no sense reflect minor aberrations. Thus their acceptance and use should prevent difficulties from arising of the kinds encountered in several recent studies where all single-needle pinyons have been assumed to be *P. monophylla*.

TAXONOMIC PROPOSALS

The present studies, made at a population level, have extended over more than a decade and have brought to light characters of a systematic nature previously unnoted or insufficiently appreciated. The results have made it expedient to describe a new species to include the single-needle pinyons of southern California and northern Baja California. To give recognition to the presence of the new species in both Mexico and the United Stated, the epithet *californiarum*, 'of the Californias', is used, thereby reflecting older geographical terminology. At the same time a new combination is made for *P. edulis* var. *fallax* by transferring it, as a subspecies, to *P. californiarum*. The following formal proposals are thus made:

1. **Pinus californiarum** D. K. Bailey, **sp. nov.**

California single-needle pinyon

Syn.: *Pinus monophylla* Torr. & Frém. *pro parte*.

Pinus parva cum fasciculis constantibus ex uno folio aciculare sed *Pino monophyllae* dissimilis quod folia angustiora (latitudines quasi-maximae 1·5, 1·7, 2·0 vs. 1·6, 1·9, 2·3 mm) habet, minus glauca et saepe longiora (longitudines quasi-maximae 4, 5, 6·25 vs. 3·75, 4·75, 5·75 cm). Vaginae fasciculorum breviores (5, 6, 7 vs. 7, 9, 11 mm) et partim deciduae maturissime. Fine primi temporis anni reliquiae vaginarum fasciculorum rosulas parvas et basales faciunt, segmentis vaginarum minus quam 270° retroversis, typice paulo plusquam 90°; rosulae tamen *Pini monophyllae* magnae, segmentis vaginarum plusquam 270° retroversis interdum usque ad 720°. Linearum stomatalium numerus plerumque 14, 18, 23 vs. 18, 24, 31. Canalium resiniferorum numerus rare minus quam 8, plerumque 9, 12, 16, in *Pino monophylla* ex contrario rare 8 excedit, plerumque 2, 4, 7 est. Coni plerumque minores et habent apophyses basales minus protuberantes et bases complanatiores. Ratio axis longitudinis pro aperti coni latere saepe minor quam 1, contrarie in *Pino monophylla* ratio saepe maior quam 1. Semina parum minora et parum tenuiores parietes habent. Praeterea endospermium multo oleosius est quam illud *Pini monophyllae* (40–60% vs. 18–28%).

Note: The sets of numbers in threes separated by commas above and in the translation below represent lower decile values, median values, and upper decile values, respectively. The term quasi-maximum is defined in the discussion of the measuring programme.

A small pine with fascicles consisting of a single acicular leaf, differing from *Pinus monophylla* in having narrower leaves (quasi-maximum widths 1·5, 1·7, 2·0 vs. 1·6, 1·9, 2·3 mm) which are less glaucous and often longer (quasi-maximum lengths 4, 5, 6·25 vs. 3·75, 4·75, 5·75 cm). Fascicle sheaths shorter (5, 6, 7 vs. 7, 9, 11 mm) and partly deciduous very early. At the end of the first season the remains of the fascicle sheaths form small basal rosettes with sheath segments reflexed less than 270° and typically little more than 90°, whereas rosettes of *Pinus monophylla* are large, with sheath segments reflexed more than 270° and sometimes as much as 720°. Stomatal lines usually 14, 18, 23 in number vs. 18, 24, 31. Number of resin ducts rarely less than 8 and usually 9, 12, 16, whereas for *Pinus monophylla* the number of resin ducts rarely exceeds 8 and is usually 2, 4, 7. Cones are commonly smaller and possess less protuberant basal apophyses and more flattened bases. The ratio of axis length to open-cone width frequently less than 1, in contrast with *Pinus monophylla* for which the ratio is frequently greater than 1. Seeds are slightly smaller and have slightly thinner seed walls. Moreover the endosperm is much oilier than that of *Pinus monophylla* (40–60% vs. 18–28%).

Type: United States, California, San Diego County, Anza-Borrego Desert State Park, northwest base of Whale Peak, Vallecito Mountains, 33°03′N 116°20′W, 1280 m, 27 iii 1981, *D. K. Bailey* 81–08 (holo. COLO; iso. ARIZ, ASU, E, K, MEXU, MO, NY, RENO, RM, TEX, UC, US, UTC).

2. Pinus californiarum subsp. **fallax** (Little) D. K. Bailey **comb. et stat. nov.**
Arizona single-needle pinyon

Syn.: *Pinus edulis* var. *fallax* Little in Phytologia 17:331 (1968). Type: Arizona, Gila County, Tonto National Forest, Sierra Ancha Experimental Forest, 4 vii 1961, *E. L. Little, Jr.* 18581 (holo. US).
P. edulis var. *monophylla* (as *monophyllus*) Torrey in Ives' Report, part 4, 28 (1860) *nom. nud.*
P. monophylla var. *tenuis* Tidestrom in Tidestrom & Kittell, Fl. Ariz. New Mex. 2 (1941) *nom. nud.*

A detailed study of *P. californiarum* subsp. *fallax* together with its geographical associates *P. edulis* and *P. remota* will be presented in Part II of this study. Table 1 provides a conspectus of the single-needle pinyons.

TABLE 1

Conspectus of the single-needle pinyons.

Character	*Pinus monophylla*	*Pinus californiarum* subsp. *californiarum*	*Pinus californiarum* subsp. *fallax*
Needles			
Length, cm	4–6	4–6	4–6
Thickness, mm	1·6–2·3	1·5–2·0	1·2–1·7
Fascicle sheath length, mm	7–11	5–7	4–7
Fascicle sheath curl-back, degrees	greater than 270	less than 270	less than 270
Number of resin ducts	2–7	9–16	2–7
Number of stomatal lines	18–31	14–23	12–20
Colour	bluish green glaucous	dark green	dark green
Cones			
Shape, dry and open	axis length often greater than width	axis length often less than width	axis length often less than width
Base	rounded with protuberant apophyses	flatter with much less protuberant apophyses	flatter with much less protuberant apophyses
Seeds, all wingless	large, with thin shells and starchy endosperms	smaller, with slightly thinner shells and oily endosperms	smaller, with slightly thinner shells and oily endosperms
Habitats			
Elevation, m	1400–2600*	1100–1600	1200–1800
Climate	dry summers and very cold winters usually with snow	dry hot summers and mild winters with some rain	hot summers with some rain and less mild winters with some rain

*Excludes four collections from the coastal counties, Santa Barbara, Ventura and Los Angeles, California, where suitable habitats occur at exceptionally low elevations ranging from 945 to 1310 m. The highest collection made was at 2870 m in Inyo County, California.

THE COLLECTING PROGRAMME

Very early in the investigations it was recognized that considerable tree-to-tree variation existed in any stand of single-needle or 2-needle pinyons. Variation is most immediately apparent in needle number counts across central Arizona into SW New Mexico, in central and SW Utah and in the New York Mountains of eastern San Bernardino County, California. After some trial collecting, beginning in December 1973, a collecting programme consisting of 10-tree samples per collection site was decided upon, and a branchlet at least 30 cm long was taken from each of the 10 trees. The figure of 10 was considered to be a practical upper limit when the subsequent time-consuming work on the specimens was taken into account. Smaller samples would only have increased the risk of fortuitously overlooking important variants. The samples were taken from trees judged to be in good condition; very small trees and trees showing evidence of excessive stress were avoided as much as possible. As a practical matter, when hundreds of trees are to be considered, an entire tree cannot be studied in detail, and the branchlet selected to represent a tree was chosen to be as fully clothed in foliage as possible, and of sufficient length to permit needle retention to be determined. This form of deliberate selection is intended to show what a tree is capable of in the production of its foliage rather than how such capability may be limited in certain parts of a tree by special circumstances. As convenient, samples were taken with strobili, but foliage, being comparatively independent of time of year, was the principal consideration. The 10-tree collections were kept in heavy brown paper bags and brought back to the laboratory for study. If kept cool and in the dark, the branchlets dried slowly, and several weeks after collecting were still fresh enough for easy study. Totally dry specimens could be used but were much more time consuming. The branchlet specimens were not pressed. Occasionally collections that could not be immediately studied were sealed in plastic bags and frozen to preserve their usefulness. Seed samples were also taken when available at selected sites.

THE COUNTING AND MEASURING PROGRAMME

In the laboratory the trees (branchlets) were studied one by one and the needle retention in years recorded though not further considered at this time. Numbers from 1 to 10 were marked on the twig ends of each collection so that a particular branchlet could be identified later in the event of any problem arising with the data extracted from it. The following steps were then taken for each branchlet:

1. A pile of fascicles was stripped from the branchlet. During this step little consideration was given to the year of the needles. Thus needles of more recent years were favoured, though every effort was made to include as many fascicles from the earlier years as possible without completely stripping them from the specimen.
2. From the pile, 200 complete fascicles were segregated in as random a manner as possible, and the needle numbers recorded.
3. The longest and thickest fascicles were then selected (often the same fascicle) and their length, l (cm), and thickness, t (mm), recorded. These quantities are defined for purposes of this study as *quasi-maximum*

values. Such values cannot be assumed to be true maxima for the entire tree. Nevertheless they represent dimensions that the tree is capable of exhibiting under favourable conditions.

4. Next, 5 complete fascicles were selected by length only and ranging from the quasi-maximum (usually several fascicles were found of about that length) down to a reasonable minimum length; malformed or poorly developed fascicles were avoided. Usually the shortest fascicle selected was about half the length of the quasi-maximum. If there was a substantial fraction of 2-needle fascicles present in a mainly single-needle collection, 5 such fascicles were also selected.
5. One by one, beginning with the longest fascicle, the needles were examined under a low-power binocular dissecting microscope using diffuse fluorescent light, and the number of stomatal rows or lines, s, midway along the needle recorded.
6. Next, the same needles were sectioned near their midpoints and, again beginning with the longest needle and using the microscope, the number of resin ducts or canals, r, recorded. The sectioning technique was very simple. Each needle was held against a small flat piece of soft wood and struck a sharp blow near its midpoint with a utility knife, a knife with a heavy handle and equipped with a replaceable razor blade. Very fresh needles occasionally tended to be crushed rather than cut cleanly. Completely dry needles tended to shatter. However several attempts, sometimes choosing a substitute needle, were usually sufficient to make the count. Partly dry needles were the most easy to section cleanly.
7. Finally, each branchlet was carefully examined for its fascicle sheaths. The typical length, fs (mm), was recorded for sheaths still clasping the most recent fascicles. The angular curl-back of the sheath tips remaining in the basal rosettes formed by slightly older sheaths was also noted in a very rough manner as typically less than or greater than 270°. In some stands, particularly those where needle-number counts suggest hybridization or introgression, the curl-back was difficult or nearly impossible to judge with the 270° dichotomy. Occasionally, depending on season and other conditions, all fascicle sheaths were split and curled back, which, because of the deciduous nature of the sheath ends, made determination of sheath length difficult or impossible. Additional observations were also recorded as seemed desirable. Examples are foliage colour when it seemed unusual, cone or conelet features as available, and the presence of the sweet odour of ethyl caprylate (characteristic only of *P. edulis*) in the cut end of the branchlet, or in crushed needles when fairly fresh. For some collections the degree of development of the winter buds when dormant was noted, especially when considerable variation was observed among the trees of the collection.

DATA ANALYSIS—DEFINING TAXA IN TERMS OF THE DATA

The numbers resulting from the programme of measurements and counts exhibit highly variable behaviour. To bring order out of the apparent chaos of numbers two steps were taken:

1. The available measurements and counts were used to formulate specifications or defining criteria for each of the three single-needle taxa, and

TABLE 2

Working definitions for taxa and component subtaxa.

1-NEEDLE TREES

Of 200 fascicles sampled per tree, the number of 2-needle fascicles is $\leqslant 20$ (i.e. 10% of the sample). A few additional trees (see Table 3 and Appendix) are included as a practical matter with >20 but $\leqslant 40$ 2-needle fascicles and are identified by asterisks. Five 1-needle fascicles are sectioned per tree for resin duct count.

Taxon and subtaxa	**Resin duct number, r**	**Stomatal row number, s**	**Fascicle sheath curl-back, cb**	**Endosperm composition**
Pinus monophylla s. s. (abbr. M)				
m	not more than 2 of 5 needles with $r > 8$	not more than 2 of 5 needles with $s < 21$	$\gtrsim 270°$	starchy
fn (less common)	same	not more than 2 of 5 needles with $s > 20$	same	same
Pinus californiarum s. s. (abbr. C)				
c	not more than 2 of 5 needles with $r < 9$	not more than 2 of 5 needles with $s > 21$	$\lesssim 270°$	very oily
ns (less common)	same	not more than 2 of 5 needles with $s < 22$	same	same
Pinus californiarum subsp. *fallax* (abbr. F)				
f	same as for m	same as for c	$\lesssim 270°$	very oily
nf (very rare)	same	same as for ns	same	oily?

2-NEEDLE TREES

Of 200 fascicles sampled per tree, the number of 1-needle fascicles is $\leqslant 20$ (i.e. 10% of the sample). A few additional trees (see Table 3 and Appendix) are included as a practical matter with >20 but $\leqslant 40$ 1-needle fascicles and are identified by asterisks. Five 2-needle fascicles are sectioned per tree for resin duct count. No subtaxa are designated.

Pinus edulis s. s. (abbr. E)				
e	all needles with $r \leqslant 2$; needles with $r = 1$ occur rarely and east of the range of this report	not more than 4 of 10 needles with total $s > 21$ for both surfaces	$\gtrsim 270°$	very oily

APPLICATION

Use of the definitions above allows the taxonomic composition of the collections to be determined. The results are shown in the Appendix in the column headed 'Determinations'. The letter abbreviations M, C, F and E identify the taxa present, and in parentheses after each letter is stated the number of trees of each of the subtaxa in the order shown above. After E only a single number is given. The letter X is used to designate indeterminate trees and, like E, is followed by a single number. Thus the sum of the numbers in the parentheses will equal the number of trees in the collection. The superscripts with asterisk indicate the number of trees within the base number for which an asterisk is appropriate. The majority of the indeterminate trees have the number of 2-needle fascicles >40 but >160, but, if the number is $\geqslant 160$, at least one of the needles in the five fascicles sectioned has more than 2 resin ducts, which suggests the influence of M, C or F. Other examples are trees having all the characters of M except for too many resin ducts suggestive of the influence of C. Two trees were found in Baja California with slightly too few resin ducts, perhaps reflecting influence of *Pinus quadrifolia* which was present in their immediate vicinity (v. Zavarin *et al.*, 1980). The locations of nearly all the indeterminate trees are such as to make the suggested influences plausible.

for *P. edulis* as present in some of the mixed collections. The final criteria were arrived at only after several years of continuing collecting, including a few repeat collections, and much trial and error. They are summarized in Table 2 where the convenient mnemonic abbreviations M, C, F and E, standing for *P. monophylla*, *P. californiarum* subsp. *californiarum*, *P. californiarum* subsp. *fallax* and *P. edulis*, respectively, are introduced. Table 2 also provides information on endosperm composition of these taxa as determined by Botkin & Shires (1948) and supplemented by results from the limited seed sampling of the collecting programme. Ranges of values representing all available data on percent of fat are provided at the end of the diagnosis for C (p. 278). Two subtaxa each are defined, for study purposes, for M, C and F. Those with the lower case letters m, c and f correspond, respectively, most nearly to the common view of each taxon, and to specimens at their type localities; the type locality for F is in central Arizona beyond the geographical area of concern in this report. Subtaxa fn, ns and nf represent departures from the more typical values of stomatal line numbers and are comparatively rare; fn represents smaller values more like those of c and f; ns and nf correspond to larger values more like those of m. The subtaxa were devised to allow variation within taxa to be examined. Two criteria, useful both in the field and in the herbarium, when taken together are sufficient to separate C from M using foliage only. These are resin duct numbers and fascicle sheath curl-back. Table 2 states the particular procedure used in this study for utilizing resin duct numbers. In practice it is sufficient to section a few needles. If the resin duct count is 9 or greater for the majority of the needles, the curl-back of the fascicle sheaths is typically less than 270°, and often only about 90°, and the basal rosette is small, the tree is C. For M the majority of counts would be 8 or less, and often much less, and the basal rosette would be large, with curl-back of at least 270°, and often much more; curl-back of as much as 720° is not uncommon. Obviously exceptions to these and other criteria of Table 2, such as an excess of 2-needle fascicles, occur for indeterminate trees for which the letter symbol X is used. F shares the same fascicle sheath characters, shortness, reduced curl-back and small basal rosettes, with C from which it differs mainly in having resin duct numbers less than or at most equal to 8, and sometimes only 2 to 4. These latter characters as a group are shared solely with *Pinus remota* among the other pinyons (Bailey & Hawksworth, 1979).

2. This step consists of applying the defining criteria to the individual trees in the 135 collections comprising this study. The results are reported in the Appendix in chronological order in the column headed 'Determinations'. The missing chronological project numbers represent pinyon collections containing no trees of M or C. The abbreviated entries are explained under the heading, Application, at the end of Table 2. Of the 135 collections, 67 are pure M, 16 pure C, and the remaining 52 collections are mixed and usually include indeterminate trees. Table 3 provides a census or summary count of the trees of the various taxa, subtaxa and indeterminate trees, totalling 1332 trees. Figures 1 and 2 show the positions of the 135 collections and identify pure and mixed collections.

TABLE 3

Census of taxa, subtaxa and indeterminate trees in the 135 collections described in the Appendix and comprising 1332 trees.

Taxon	**Subtaxa**		**Sums**	**Subtaxa**		**Sums**	
M	m	fn		m*	fn*		*total* M
	664	137	801	21	10	31	832
C	c	ns		c*	ns*		*total* C
	223	42	265	9	—	9	274
F	f	nf		f*	nf*		*total* F
	84	4	88	8	—	8	96
E	e			e*			*total* E
	19		19	5		5	24
			1173			53	

TOTAL of determinate trees	1226
TOTAL of indeterminate trees (*total* X)	106

If all trees of subtaxa identified by an asterisk, together with trees of nf, are transferred to indeterminate status, the total of determinate trees would be reduced to 1169 and indeterminate trees increased to 163.

DATA ANALYSIS—DISTRIBUTIONS OF MEASUREMENTS AND COUNTS

With taxonomic determinations available for about 92% of the trees sampled, it becomes possible to determine separately for M and C the distribution of:

1. The typical values of fascicle sheath lengths (fs) to the nearest mm, represented by one value per tree for those trees for which it was measurable at the season of the collecting.
2. The quasi-maximum needle lengths (l) to the nearest 0·25 cm, and needle thicknesses (t) to the nearest 0·1 mm, represented by one value each per tree.
3. The counts of resin duct numbers (r) and stomatal line numbers (s), represented by 5 values each per tree.

The results are normalized as percentages to facilitate comparisons, but the actual numbers may be recovered by using the various totals stated in the figure captions. Because it would be inconvenient to prepare the figures as histograms, the points are connected by straight lines between the midpoints of the class intervals. The lower decile, median, and upper decile values derived for M and C, as found in all collections whether pure or mixed, are shown by enlarged dots in the appropriate figures beginning with Fig. 3. These values are expressed numerically in the diagnosis for C, and in Table 1 which states only interdecile ranges.

MEASUREMENTS

Figure 3 demonstrates the significantly longer fascicle sheaths of M as compared with C; it also shows a limited region of overlap between 6 and 8 mm. Thus fascicle sheath lengths of less than 6 mm almost certainly describe C, whereas those longer than 8 mm describe M. The curl-back character is related to the fascicle sheath length, but involves some uncertainty since

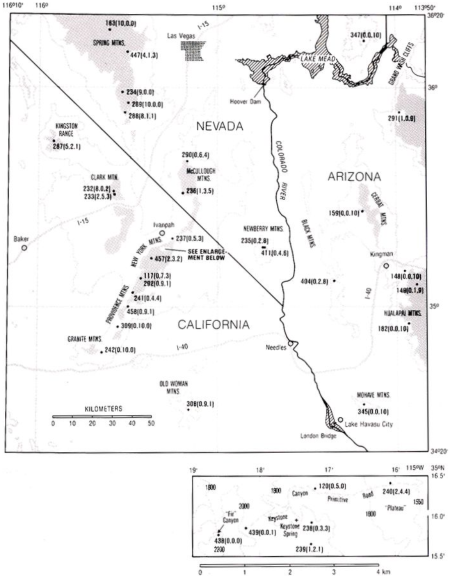

FIG. 2. Geographical positions and related topography for all the pinyon collections of the project made on both sides of the Colorado River from the vicinity of Lake Mead southward to latitude 34°20′N with particular emphasis on the complicated situation in the New York and nearby mountains (see enlarged section). The precise location for collection 120 is somewhat uncertain. Contours shown for 1000 and 1500 m with higher ground within the 1500 m contour shaded gray. Collections 148, 159, 182, 345 and 347, consisting entirely of *Pinus californiarum* subsp. *fallax* (F), are included for completeness though not given in the Appendix. Each collection is identified by its collection number followed by a group of three numbers in parentheses which represent respectively the number of trees of M, C and F. The sum of these numbers will be 10 except when there are indeterminate trees (X) or trees of *P. edulis* (E) present.

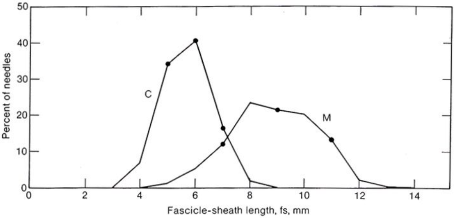

FIG. 3. Normalized distributions of fascicle sheath lengths (fs) using all available measurements; 247 and 251 needles for M and C respectively.

the distal portions of the sheaths are shed before curl-back is complete, and it is suspected that the fraction shed is not the same for the two taxa. This raises the possibility that curl-back and sheath length may be independent characters and is a matter that would benefit from further study.

Needle dimensions are represented in Figs 4 and 5. Figure 4 shows that C has slightly longer needles than M, but with a very large overlap which renders needle length alone of little value as a distinguishing character. However Fig. 5 shows that C has distinctly thinner needles than M. Needle thickness for M shows a consistently present double peak or bimodal distribution for which an explanation has yet to be found.

It was noted repeatedly during the collection stage of the project that the needles of C, especially in pure stands lacking the characteristic glaucousness of the needles of M, were distinctly finer. In mixed stands, such as found in the New York Mountains and on Clark Mountain, single-needle trees with foliage varying from clear green, such as is found in E, to conspicuous bluish green as found in M occur side by side. The greater number of whitish stomatal rows found on M, and more particularly on m as distinguished from fn, is sometimes cited as the reason for the apparent glaucousness. This is only partly correct; the epidermal tissue of M, like that of *Pinus quadrifolia*, is obviously of a lighter (or more bluish) green than that of C when compared under a microscope using fresh material. Glaucousness is clearly an unreliable character in mixed stands.

Fineness can be defined as the ratio of needle length to fascicle thickness, l/t, usually in the same units, and is therefore a dimensionless quantity. It would have been ideal if l/t had been determined for each of the five fascicles selected to represent each tree for counts of r and s. This was not done. However, for illustrative purposes the percentile values of l and t may be used. The results are shown in Table 4 which illustrates that the needles of C are consistently finer than those of M regardless of the variation in needle dimensions, and while longer needles of both taxa are systematically thicker, the longer needles of C are finer by about 25% than those of M. The fineness difference is less for the median and shorter needles.

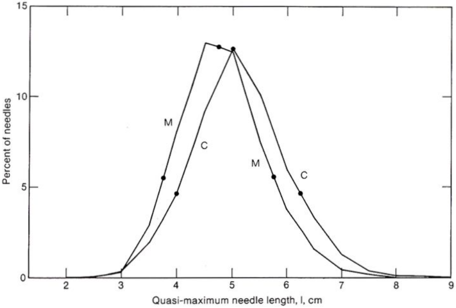

FIG. 4. Normalized distributions of quasi-maximum needle lengths (l) for all M and all C; 832 and 274 needles respectively. Corresponding normalized distributions for all m and c are almost indistinguishable and therefore not shown.

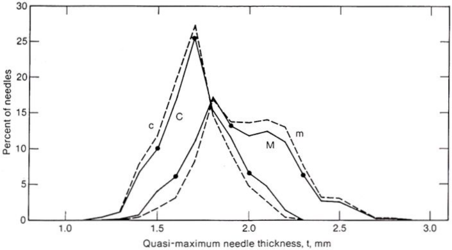

FIG. 5. Normalized distributions of quasi-maximum needle thickness (t) for all M and C (continuous lines), 832 and 274 needles respectively; compared with similar distributions of m and c (broken lines), 685 and 232 needles respectively.

TABLE 4

Needle fineness, l/t, for C in relation to M.

	M			C			
	l, mm	**t, mm**	**l/t**	**l, mm**	**t, mm**	**l/t**	**C vs. M % finer**
Lower decile	37·5	1·6	23·4	40·0	1·5	26·7	14·1
Median	47·5	1·9	25·0	50·0	1·7	29·4	17·6
Upper decile	57·5	2·3	25·0	62·5	2·0	31·2	24·8

COUNTS

Figures 6, 7, and 8 are concerned with the distribution of resin duct numbers, r. Fig. 6 is of particular importance as it demonstrates convincingly the usefulness of r in segregating C from M. Figure 7 shows the distributions for the subtaxa of M and C. It will be seen that the plots for m and c differ only slightly from those for M and C of Fig. 6, whereas those for fn and ns show greater separation. The separation of fn is in the direction of plots for F, to be shown later in Part 2. The plot for ns, though based on limited data, exaggerates the difference between the taxa. Figure 8 compares the distributions of M and C for pure and mixed stands where evidence of gene exchange must be expected to show in the distributions for mixed stands. Such an effect is apparent for C in the direction of M, but for M, the effect, using all the data, illustrates mainly that the shift toward E and F overcomes the shift toward C. Fortunately the two shifts can be separated since any shift toward C is unlikely to be important to the north of the extreme northern range of C. The northernmost trees of C were found in collections 443 and 447 which are situated in a sheltered locality near the east base of the southern Spring Mountains at latitude 36°10′N. Mixed collections farther north, and mainly in western Utah, might be expected to exhibit shift toward F and E. The latitude of the top edge of Fig. 2, 36°20′N, was adopted as separating the two influences, and two separate distributions for r, one on each side of that limit, were prepared. The results are shown in Fig. 9 where the two distributions are appropriately labelled N and S. The original combined distribution of Fig. 8 is repeated for comparison. The shift toward C is now seen clearly in the southern distribution, and that toward F and E, though less striking, shows in the northern distribution.

Figures 10 and 11 are concerned with distributions of stomatal line numbers, s. The effect of plotting distributions for the more usual and typical subtaxon separately from the entire taxon is illustrated in Fig. 10, where it will be seen that the overlap of the distributions for m and c is distinctly less than that for M and C. This is as would be expected from the exclusion of fn from M and ns from C. It will also be seen that the distributions cross at about s = 21 as is required by the defining criteria of Table 2. Figure 11 illustrates the different distributions for pure and mixed stands. For M the majority of the pure stands occur far from the contact regions. In and near the contact regions there are not only marked increases in the occurrence of the subtaxon fn, but evidence of some shift toward E and F in Utah, and toward C in southern Nevada and immediately adjacent California to the south. These shifts are seen to be strong for M in mixed stands, but less so for C.

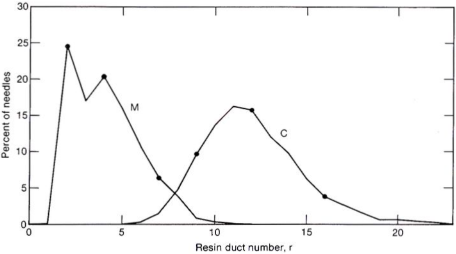

FIG. 6. Normalized distributions of resin duct number (r) for all M and C; 4160 and 1370 needles respectively. Corresponding normalized distributions for all m and c are almost indistinguishable and therefore not shown.

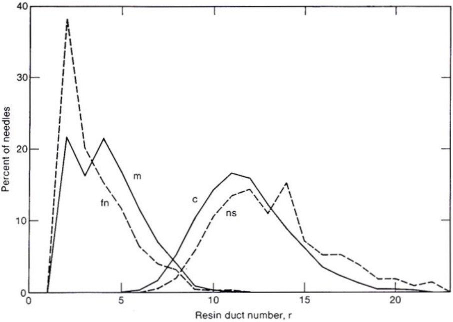

FIG. 7. Normalized distributions of resin duct number (r) for all m and c (continuous lines), 3425 and 1160 needles respectively; compared with similar distributions of fn and ns (broken lines), 735 and 210 needles respectively.

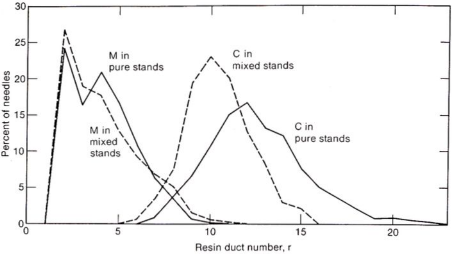

FIG. 8. Normalized distributions of resin duct numbers (r) from M and C from pure stands only (continuous lines), 3335 and 1035 needles respectively; compared with similar distributions from mixed stands (broken lines), 825 and 335 needles respectively.

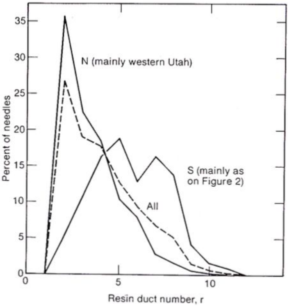

FIG. 9. Normalized distributions of resin duct numbers (r) for all M from mixed stands (broken lines), 825 needles; compared with similar distributions of M in mixed stands north and south of 36°20′N (continuous lines labelled N and S), 585 and 240 needles respectively.

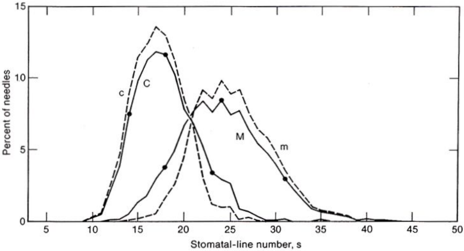

FIG. 10. Normalized distributions of stomatal line numbers (s) for all M and C (continuous lines), 4160 and 1370 needles respectively; compared with similar distributions for m and c (broken lines), 3425 and 1160 needles respectively.

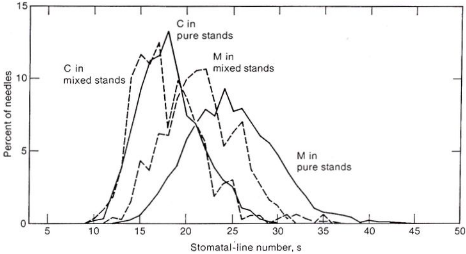

FIG. 11. Normalized distributions of stomatal line numbers, (s) for M and C from pure stands only (continuous lines), 3335 and 1035 needles respectively; compared with similar distributions from mixed stands (broken lines), 825 and 335 needles respectively.

It is difficult at this stage of the study to decide whether the various shifts or distortions from otherwise typical distributions reflect gene exchange or some climatic or edaphic influence. Some gene exchange clearly does take place as indicated by the numerous indeterminate trees in and near the contact regions. There is little doubt, owing to the effort to be as definite as possible, that several of the indicated determinations in and near the contact regions might better have been included in X, especially when the decision was taken ultimately on the basis of curl-back. In this respect Table 3 should also be noted.

The following additional results from the counting programme for r and s are insufficiently emphasized in Figs 6 and 10. The greatest number of resin ducts found in a single needle was 23. The needle occurred in collection 307 consisting entirely of trees of *P. californiarum* from the foothills at the eastern end of the San Bernadino Mountains of southern California. The greatest number of stomatal lines on a single needle was 49. This needle occurred in collection 312 consisting entirely of trees of *P. monophylla* from south central Nevada. Each of these extreme values represents a character, large number of resin ducts, and large number of stomatal lines, unique to the species in which it occurs, and at the same time unique in *Pinus*. Another result which came as a surprise, and also rare but probably not unique in *Pinus*, was the finding of occasional needles in *P. californiarum* having more resin ducts than stomatal lines.

AREAS OF MAXIMUM TAXONOMIC COMPLEXITY

With the results now available it is possible to make progress in understanding the complex situation in the New York Mountains where both single-needle and 2-needle trees are present. Wolf (1938, p. 45) seems to have been the first to report there the presence of *Pinus edulis*. It remained for Henrickson & Prigge (1975) to report the presence there also of *Abies concolor*. The situation on Clark Mountain is complex as well but, without 2-needle trees, the complexity within the single-needle trees has escaped much attention. *Abies concolor* is also present on Clark Mountain as was indeed reported by Wolf (loc. cit.). These two relict stands of *Abies* on cold north slopes say much about the climate, seasonal variation of temperature and precipitation, both present and past, at the two stations only about 40 km apart. *Abies* is well known and more abundantly present in the higher and more massive Spring Mountains where it first occurs about 45 km north of Clark Mountain. *Abies* is also reported from the Kingston Range (Henrickson & Prigge, 1975,p.165).

CLARK MOUNTAIN

Collection 232, made on the secondary summit ridge about 1·6 km east of the main summit, consisted of 8 trees of M and 2 doubtfully of F. More detailed collecting and study will probably show that all trees near the summit are M. Collection 233 made some 550 m lower on the south slopes consisted of 2 trees of M, 5 of C and 3 of F. At the lower site both glaucous and clear green trees occurred and C was evident, though entirely absent at the higher site. The presence of trees well to the west of the Colorado River determinable as F by the criteria of Table 2 came as somewhat of a geographical surprise.

C is a taxon of warmer and drier stations than M, and its absence at the upper station seemed normal. M, on the other hand, is a tree of much colder environments and usually of little winter precipitation mainly in the form of snow. F is somewhat intermediate in respect to its climatic requirements and its presence from the climatic viewpoint at the lower site did not seem unusual. In Arizona it occurs just below the cold regimes of the Mogollon Rim and Plateau, but above the very warm and winter-dry regimes which suit C so well in California. The substantial reduction in M at the lower site would seem to be a result of too dry a climate. This interpretation is in accordance with the general distribution of M shown in Fig. 1.

NEW YORK MOUNTAINS

The pinyons of these mountains, especially near the highest but unnamed peak at the north end of the range, present the most complex set of characters found anywhere in the study area represented in Fig. 1. Details are shown on fig. 2. The primitive road into Keystone Canyon provides access. Collection 240 on the Plateau (Roof's name) included the site of fig. 2 of Roof (1978). Indeed the prominent tree in the center of his photograph was selected as one of the 10 trees sampled. Roof was emphatic in the figure caption that, though single-needled, it was not *P. monophylla*. The results of this study agree; the tree belongs to the subtaxon ns of C.

The presence of 2-needle trees with green or slightly glaucous foliage in these mountains requires careful study. First of all many past reports and collections have simply assigned any pinyons having predominantly 2-needle fascicles to *P. edulis* without regard to resin duct numbers. Thus Martínez (1948), finding 2-needle fascicles among the pinyons of northern Baja California, believed that he had found *P. edulis*. He illustrates this with two cross-sections of needles from 2-needle fascicles (figs 53 and 54). The first shows 2 resin ducts and almost certainly represents the somewhat infrequent form of *P. quadrifolia* with mainly 2-needle fascicles with 2 resin ducts and several dorsal stomata reflecting some introgression from C. The second figure represents a cross-section of a needle with 9 resin ducts from the rare 2-needle fascicles to be found among the single-needle fascicles of any specimen of *P. californiarum* subsp. *californiarum*. Other examples have been found in material now known as *P. remota* from west Texas and northern Mexico. It is not surprising that these precedents were followed by Trombulak & Cody (1980) who, in their study of the pinyons of the New York Mountains, concentrated their attention on needle number. They found the pinyons at higher elevations to have mostly 2-needle fascicles while those at lower elevations had mainly single needles. Trees in the intermediate zone had both single-needle and 2-needle fascicles on the same tree in differing proportions, but rarely very evenly divided (the findings of this study confirm this). They therefore decided to classify their pinyons as either *P. edulis* or *P. monophylla* according to the predominant needle number. Had they but studied the trees of Clark Mountain, they might have realized the error of their interpretation in their closing paragraph which states that 'The altitude zonation exhibited by *P. edulis* and *P. monophylla* can then be interpreted as the superiority of *P. edulis* in cooler, wetter environments and the superiority of *P. monophylla* in hotter, drier environments.' By substituting *P. californiarum* subsp. *calforniarum* for *P. monophylla* their interpretation would have been correct. A still more recent study by des Lauriers & Ikeda (1986), though taking full account of resin duct numbers, falls into the same taxonomic trap. Moreover, by limiting the study area to the New York Mountains it fails to benefit from examination of the other mainly single-needle pinyons in the surrounding areas as shown in Fig. 2.

In the early stages of collecting in the New York Mountains, two collections, numbered 238 and 239, were found to have 4 and 6 trees respectively that fell into the indeterminate category. Several of these trees had a high fraction of 2-needle fascicles, and one was entirely 2-needled; it was taken to be *P. edulis* before it was closely studied in the laboratory. Instead of having exclusively 2 resin ducts per needle as required for E, its counts were mainly 6's and 7's with only one needle of those sectioned with 2. The curl-back of its fascicle sheaths was much less than 270°, and therefore typical of C. Lanner (1974) recognized the resin duct problem but did not pursue the matter. Wells (P. V. Wells, pers. comm., 1984) climbed to the highest points of the mountains and near the head of Fir Canyon (Wells' name) where he found many trees that appeared to be genuine E. Collections 438 and 439 of the present study were made to test this finding. Collection 438, made at the head of and slightly down into the very steep north facing Fir Canyon, only 0·5 km north of the highest peak, contained 5 trees of unmistakably pure E and 5 indeterminate trees. Thus the 5 pure trees all had exclusively 2 resin ducts per needle, whereas the other trees, while having almost all 2-needle fascicles, exhibited more than 2 resin ducts in nearly all needles sectioned. The final and convincing confirmation that pure E was present was the very noticeable odor of ethyl caprylate in the freshly cut branchlet ends and in crushed needles. Collection 439 only about 0·6 km east northeast of 438, but 260 m lower, illustrates how rapidly E disappears with decreasing elevation. All but 2 of the 10 trees from the lower site had a majority of 2-needle fascicles, and two of them had 200 2-needle fascicles out of 200 fascicles. All 10 of the trees had needles with more than 2 resin ducts; one of them had a sufficient number of single-needle fascicles to qualify as F; none of the needles sectioned had a resin duct number exceeding 6. Proceeding to lower elevations, as shown in Fig. 2, trees with predominantly 2-needle fascicles became rarer, and trees of C and F grew in number among the many indeterminate trees. A very few trees qualified, somewhat shakily, as M.

Study of Fig. 2 shows that trees of F decrease in frequency of occurrence with distance from the New York Mountains and entirely disappear west of the Colorado River north of collection 447, west of 287 and south of 308. To the east, however, the frequency rises sharply as illustrated by the two collections from the Newberry Mountains, numbers 235 and 411. East of the Colorado River no collections had less than 8 trees of F, and only 3 trees of C were found, 2 in collection 404 and 1, anomalously, in collection 149. C evidently cannot succeed in the mountains on the Arizona side of the river where there is substantially more summer rain than is present in its usual habitats.

PHYTOGEOGRAPHICAL CONCLUSIONS

PAST DISTRIBUTIONS

During the last pleniglacial period, which came to a rapid end between about 11000 and 8000 years ago, the climate was both cooler and wetter in the area of Fig. 1, and M was confined to refugia located near the southern limits of its present distribution. Based on radio-carbon dating of preserved organic matter from ancient packrat (*Neotoma* spp.) middens containing single-needle pinyon material, M did not then occur north of the Scodie Mountains (35°36′N) of Kern County, California, near the present collection 161, and north of the Sheep Range (36°38′N) of Clark County, Nevada, near the present collection 088. At the same time E, at its westward limits, was absent from Utah but present in Arizona, finding refuge, for example, at lower elevations at the western end of Grand Canyon (36°07′N), and somewhat farther east (35°43′N) (Van Devender & Spaulding, 1979, p. 705). E also reached or possibly remained on mountains on both sides of the lower Colorado River, that portion of the river below Lake Mead, at least as far south as the New York Mountains. Occasional trees with 2-needle fascicles present in more than half the fascicles still occur as far south as collection 241 (35°03′N) and as far north as collection 234 (35°59′N) as shown in Fig. 2. These collections suggest that the New York Mountains in the past were not the exclusive preserve of E west of the Colorado River. With the warming and drying that accompanied the glacial retreat the New York Mountains, alone, maintained significant E, but only at the highest elevations, as previously discussed. M today extends southward to the summit area and north facing slopes of Clark Mountain, and a few additional specimens have been found in mixed stands in the New York Mountains as far south as collection 457 (35°13′N). Still farther south the land is significantly lower, and the climate in the less massive mountains there was probably too warm and dry even during full glaciation to support M.

The post-glacial warming allowed M to expand its range northward with surprising rapidity, as is revealed by the rat-midden studies already cited, while remaining with some altitudinal adjustments near its present southern limits. At the same time E, which requires considerably more summer precipitation than M, disappeared west of the lower Colorado River except in the New York Mountains while C, moving northward, invaded the lower skirts of the higher mountains, reaching in sheltered locations, as far north as collection 447 (36°10′N). The stands of E nearest the New York Mountains at the present time are in Arizona approximately 200 km to the east.

During the pleniglacial period single-needle pinyons, known or presumed to be F, existed on the Arizona side of the lower Colorado River at several locations far to the south of their present distribution. Some of these pinyons reached stations south of the Gila River, such as the Ajo Mountains just east of the Organ Pipe Cactus National Monument at 975 m elevation (Van Devender & Spaulding, 1979, p. 704), and the Tinajas Atlas at 550 m southeast of Yuma near the border of Mexico (Van Devender *et al.*, 1985, p. 611). At only three of these Pleistocene localities however were resin duct counts made which confirmed that the needles were of F and not C (Lanner & Van Devender, 1974, p. 207). E during this time presumably occupied territory now suitable for F. These and other collections demonstrate that pinyon habitats during the pleniglacial times were depressed in elevation relative to elevations today by approximately 500 m, but with anomalously greater depression farther south (Wells, 1979, pp. 318–320). It seems unlikely, however, that C was ever present along the lower Colorado River south of about 34°N though it was undoubtedly present farther west in southern California and in northern Baja

California. It is possible that the pleniglacial pinyon material found in the Turtle and Whipple Mountains north of 34° and just west of the Colorado River in California could consist of both C and F, as is the present situation farther north in the Newberry Mountains of extreme southern Nevada, but no resin duct counts seem to have been made for this material.

EVOLUTIONARY STATUS OF SINGLE-NEEDLE PINYONS

The limited sampling provided by pinyon material from pleniglacial packrat middens, extending back about 20000 years, provides no evidence of evolutionary changes in M and F, but there remains a lack of comparable material for C. However F poses some problems, the principal one of which is to explain how it maintains its single-needle stability, together with its resin duct and fascicle sheath characters at elevations below those at which it freely hybridizes with E.

Information in varying detail concerning the modern pinyon populations in the New York Mountains is provided by the collections of Trombulak & Cody (1980), the collections extending up Caruthers Canyon reported by des Lauriers & Ikeda (1986) and the collections of the present study extending up Keystone Canyon from the Plateau to the head of Fir Canyon. The data derived from these collections are in sufficient agreement, when comparisons are possible, to permit some general conclusions, and to shed light on a possible origin of F. The relict population of E at its farthest west locality holds the key to the hypothesis now formulated.

Whenever C began to return to the base of the New York Mountains at elevations as low as about 1300 m on north-facing slopes, and to other mountains nearby where E may have existed at the suitably high elevations, hybridization became possible by means of wind distribution of pollen from C at low elevations upward to E and at the same time pollen rain from E would have reached C about 700 m lower. This assumes that anthesis occurs at about the same time, but if C should flower significantly earlier than E because of its warmer environment hybridization could still have taken place between trees of E occurring at lower and moister than typical sites, and trees of C occurring at higher than typical sites such that flowering times might overlap. Once F1 hybrids occurred backcrossing in both directions and intercrosses would fairly rapidly generate a hybrid swarm encompassing the entire altitude range between E and the early arriving C. The hybrid trees which resulted at the highest levels, particularly above 1900 m at the present time, have preserved the 2-needle character of E, but often exhibit more than 2 resin ducts per needle. Below about 1750 m trees with mainly single-needle fascicles begin to predominate, reflecting genotypic selection of single-needle trees in the drier habitats where greater moisture conservation is achieved by reduction of surface area for single-needle fascicles as compared with 2-needle fascicles of the same volume. This principle was demonstrated for *Pinus ponderosa* Lawson by Haller (1965). Those trees remaining with mainly 2-needle fascicles invariably exhibit two characters associated with C, reduced fascicle sheath curl-back, and more than 2 resin ducts per needle, sometimes as many as 6 or 7. Trees with more than about 80% single-needle fascicles, have resin duct and fascicle sheath characters of both C and F, thus demonstrating that new trees of F, or trees having characters of F as specified in Table 2, are being produced in the New York Mountains at the present time.

If, instead, these trees of F had originated in Arizona or SW Utah at some earlier time and subsequently found their way to the New York Mountains, it would be extremely difficult to explain their resin duct numbers and reduced fascicle sheath characters by direct derivation from E. Derivation from M would be about as difficult to accept, notwithstanding the similarity in resin duct numbers, because of the differences in fascicle sheath characters, endosperm composition, and habitat requirements. This argument notwithstanding, some influence of M remains in the New York Mountains in the form of single-needle trees with thicker and more glaucous needles, and with much greater fascicle sheath curl-back than either C or F. Their endosperm composition is unknown at present.

Two corridors can be provisionally identified which would permit the migration of F from California into Arizona by means of a series of suitable mountain habitats separated by distances from less than 50 to about 100 km. During the pleniglacial period such a route probably existed from the Old Woman Mountains via the Turtle and Whipple Mountains of extreme eastern California across the Colorado River to the Mohave Mountains to the north, and to the New Water and Kofa Mountains to the south. Another such corridor that may still permit eastward migration can be seen in Fig. 2. It extends from the New York Mountains via the Newberry Mountains in Nevada and on across the river to the Black Mountains, and beyond to the Hualapais and northward to the Cerbat Mountains. Indeed it is probable that this corridor allowed the very limited migration of C into Arizona as shown in collection 404.

The presence of F in southwestern Arizona during the recent pleniglacial period can be explained tentatively in at least four ways, though evidence now available is insufficient to suggest strong preferences among them.

1. F was generated in New York Mountains as at present, but during an earlier warm period during which it reached Arizona by means of the northern corridor before the recent pleniglacial period could force it southward.
2. F, having been generated during an early warm period in or near the New York Mountains, moved during the pleniglacial period to much lower stations near the Colorado River and managed to cross into Arizona by the northern corridor, and thence southward; C may have accompanied this move part-way. This possibility is supported by the known presence of undetermined single-needle pinyon material in the Newberry Mountains at elevations of 730 and 850 m during the recent pleniglacial period (Van Devender & Spaulding, 1979).
3. F was generated in the New York Mountains as above, but during an earlier warm period, and was forced southward on the California side of the Colorado River with the approach of full glaciation, crossing into Arizona by the now inactive southern corridor through the Turtle and Whipple Mountains.
4. F was generated by the same process but during pleniglacial times at a location or locations in California south of the New York Mountains where E might have established a foothold in lower mountains and where C could still be present at much lower elevations. F from such sources could use the now inactive southern corridor into Arizona. The Old Woman Mountains seem a likely candidate for E in pleniglacial times, and

> for C as well at the low elevations at the south end of the range. F is still present in the Old Woman Mountains but is comparatively rare compared with C.

Ideas such as those above or combinations of them, to explain the presence of F in southern Arizona during the recent pleniglacial period, make it necessary to assume a much earlier evolutionary origin for F than its production today in the New York Mountains. The present situation only suggests the means whereby evolutionary branching from C might have started. The rarity of F today in California south of Mid Hills, between the New York and Providence Mountains, can be interpreted as the result of too dry a climate. Ancient packrat midden material from the Old Woman Mountains, should it reveal the presence of E, would be of help in evaluating the possibilities above.

It is now necessary to consider how the widespread distribution of an apparently stable F might have come about from a source or sources lying west of the lower Colorado River. If it is assumed that bird transport of the wingless seeds (Vander Wall & Balda, 1977) coupled with pollen drift on prevailing winds toward the east where more moisture is available and the winters remain mild, it would follow that F, proceeding southeastward across Arizona and also northward at low elevations near the Virgin River into southwest Utah, would show still further reduction in resin duct counts, since the influence of backcrossing with C would decrease as the distance from C increased. Backcrossing with E would account for the indeterminate trees with some or many 2-needle fascicles at intermediate elevations. The effect of such backcrossing, which takes place at present just below the Mogollon Rim, extending from northwestern Arizona to southwestern New Mexico, would be to reduce still further the resin duct counts of F at lower elevations. A few possible exceptions occur at the very low and dry elevations or at higher stations near the Colorado River (example in collection 149) where the resin duct character of C may still be capable of limited expression.

The Hualapai Mountains provide a useful piece of evidence showing that F can become stable in its single-needle character, through what may be interpreted as the complete elimination of genes giving rise to 2-needle fascicles. In the Hualapais and in the southwestern end of the Virgin Mountains in Nevada, it is possible to demonstrate that F does not depend for its single-needle fascicles on continuing genotypic elimination of 2-needle fascicles resulting from introgression from nearby E. At these localities F shows no trace of an increasing number of 2-needle fascicles with increasing elevation. In the Hualapais, except for the one tree of C in collection 149, all trees are F in collections at 1235 m, 1340 m, and 1950 m. A remarkable collection of pure F consisting of a single tree in an exposed and isolated rocky crevice was found at 2440 m, a record for the taxon. The nearest trees of E to the west of the Hualapais are in the New York Mountains 125 km away, a distance that must be presumed too large for viable pollen transport or direct seed transport. Trees of E are found much nearer at about 50 km, but downwind to the east. The Virgin Mountains collections were of pure F and ranged over elevations from 1280 to 1950 m. From these trees the nearest trees of E are found at about 57 km to the east. While F can be explained as a derivative of C influenced by E, an evolutionary process giving rise to the separation between M and C has not been suggested by the data collected for this study.

These last conjectures and conclusions are the proper subject of Part II, where they will be developed and demonstrated in detail. It is sufficient now to observe that F beyond California is a stable entity derived mainly from C, but with a residual influence of E expressed as a reduction, relative to C, in resin duct numbers. The influence of the very high resin duct counts of C is eliminated through introgressive dilution with increasing distance from California, and continuing slight introgression from E. These arguments are considered persuasive for transferring *P. edulis* var. *fallax* to *P. californiarum* as a subspecies. The taxonomic proposals may, however, be regarded primarily as a convenience reflecting the increased understanding of the single-needle pinyons.

In closing this, the first part of a continuing study, it is pointed out that the lowlands of the lower Colorado River provide an important barrier separating F from C just as the lowlands of the upper Colorado River including the Grand Canyon provide a barrier separating *Pinus aristata* Engelm. from *P. longaeva* D. K. Bailey (Bailey, 1970, pp. 237–240). It is a pity that fossil evidence of single-needle pinyons has not yet been found farther back in time than the late Pleistocene to shed light on the time and place of their origin.

ACKNOWLEDGEMENTS

The effort represented by this study has depended on no grants-in-aid of any kind, but much is owed to many persons who have voluntarily co-operated with the author in various ways involving especially the contribution of their time. In particular, thanks are due to the persons listed at the end of the Appendix whose efforts contributed much to the collecting programme. Among them the extensive efforts of E. C. Rockwell of the U.S. Forest Service, and his frequent companion in the field, W. E. Horn, must be singled out for special thanks. G. W. Welsh of the Arizona Game and Fish Department is particularly thanked for making the very difficult collection 404. Margaret Williams of Sparks, Nevada, is thanked for providing specific information on the location of a small and isolated population of M from which collection 361 was made. Particular thanks are also expressed to the Director of the White Mountain Research Station, University of California, for making available the helicopter used to make collection 015. The assistance of Dr F. C. Vasek, University of California, Riverside, was of extreme importance. Through his collection of seed material of C at several localities in southern California, it was possible to establish firmly the highly significant difference in endosperm composition between M and C. K. Snajberk of the Forest Products Laboratory, University of California, Berkeley, is thanked for the determinations of endosperm composition from the Vasek collections, and one by the author and for an additional collection of his own of M. He also provided some seed-shell thickness measurements for both taxa. Thanks are due to the National Park Service and other governmental bodies for permissions to collect on lands within their jurisdictions. Dr F. G. Hawksworth of the U.S. Forest Service provided much assistance throughout: in the form of wise counsel and criticism, the preparation for distribution of the type material of C, and for the use of the binocular microscope and fluorescent light. Dr W. B. Critchfield made an extremely valuable suggestion early in the project which shaped its further development, and Prof. P. V. Wells provided much useful discussion and occasional criticism of some of the new ideas during the course of their development. Prof. J. N. Hough is thanked for translating into Latin the diagnosis. Finally, thanks are expressed to the curators of herbaria, mainly ARIZ, ASU, CAS, E, JEPS, K, RENO, UC, UTC and US for access to relevant collections, and at the same time apologies are offered for not specifically citing their collections. In the preparation of the final manuscript, the contribution of T. P. Koeberle of a word processor, and its skillful use by Margaret Wilson must be mentioned.

Appendix

Details of the 135 pinyon collections, all but three of which consist of a branchlet c.35 cm long from each of 10 different trees. Collections 301, 429(2) and 443 contain 3, 7 and 2 branchlets respectively. All collections except 438 and 439 contain at least one branchlet determinable according to Table 2 as M or C. The two exceptions are included for their importance in understanding the pinyons of the New York Mountains.

Coll. No.	Determinations	Locality	County, State	Lat. (N)	Long. (W)	Elev. (m)	Collectors	Date
002	M(10, 0)	Snake Range nr. Lehman Caves Nat. Mon.	White Pine, Nevada	39°00′	114°12′	2010	G & P	11 i 74
013	M(5, 5)	In triangle at junction of US 6 and Ut 36	Juab, Utah	39°56′	112°09′	1860	B	22 iv 75
014	M(10, 0)	White Mts, Grand View Camp Ground	Inyo, California	37°20′	118°12′	2620	B, R, & Mi	2 v 75
015	M(10, 0)	Tin Mt, summit area, Death Valley Nat. Mon.	Inyo, California	36°53′	117°28′	2650	B	6 v 75
025	M(4, 3^{1}*)X(3)	Central Wah Wah Mts	Beaver, Utah	38°18′	113°37′	2650	B & Wa	14 vii 75
040	M(10, 0)	Sierra Nevada, 3 km N of Markleeville	Alpine, California	38°43′	119°47′	1830	B	9 v 76
065	M(3, 7)	15 km E of Panaca along Nev 319	Lincoln, Nevada	37°47′	114°15′	1845	Z	14 viii 76
088	M(9, 1)	Sheep Range, Deadman Canyon	Clark, Nevada	36°37′	115°15′	2135	B, R, & H	15 x 76
089	M(8, 2)	21 km NE of Oasis along Nev 233	Elko, Nevada	41°08′	114°18′	1740	B	20 x 76
112	C(7, 3)	Vallecito Mts, Whale Peak, Anza-Borrego Desert State Park	San Diego, California	33°01′	116°19′	1525	Sn	18 iii 77
117	C(7, 0)F(3^{1}*, 0)	Providence Mts, Mid Hills Camp Ground	San Bernardino, California	35°08′	115°26′	1700	Sn	23 iii 77
120	C(5^{2}*, 0)X(5)	New York Mts, Keystone Canyon	San Bernardino, California	35°16′	115°17′	1660	Sn	24 iii 77
137	M(7, 2)X(1)	Confusion Mts, just S of US 6/50	Millard, Utah	39°03′	113°35′	2255	B & Wa	12 vii 77
138	M(9^{1}*, 1)	City of Rocks State Park, Twin Sisters Picnic Ground	Cassia, Idaho	42°04′	113°44′	1875	B & Su	28 vii 77
145	M(10, 0)	Glass Mountains, Sawmill Meadow Road	Mono, California	37°50′	118°41′	2350	B & R	11 x 77
149	C(1, 0)F(9, 0)	Hualapai Mts, Hualapai Mt Park, above Camp Ground	Mohave, Arizona	35°06′	113°53′	1950	B	17 x 77

APPENDIX—*continued*

Coll. No.	Determinations	Locality	County, State	Lat. (N)	Long. (W)	Elev. (m)	Collectors	Date
150	M(9, 1)	1 km N of US 6 along Ellison Creek Road	Nye, Nevada	38°49′	115°21′	1950	B	21 x 77
151	M(6^{1}*, 2)X(2)	Northern Wah Wah Mts, crest of Ut 21	Beaver, Utah	38°31′	113°33′	1965	B	22 x 77
152	M(5^{1}*, 3)E(1^{1}*)X(1)	San Francisco Mts, Frisco townsite along Ut 21	Beaver, Utah	38°27′	113°16′	1995	B	22 x 77
155	M(10, 0)	Panamint Mts, Wild Rose Canyon, Thorndike Camp Ground, Death Valley Nat. Mon.	Inyo, California	36°14′	117°04′	2285	B	24 xi 77
161	M(10, 0)	Sierra Nevada, Walker Pass	Kern, California	35°39′	118°02′	1615	R	2 xii 77
163	M(10, 0)	Lida Summit, S of Nev 266	Esmeralda, Nevada	37°26′	117°34′	2285	R	20 ii 78
164	M(9, 1)	White Mts, Cedar Flat, Westgard Pass	Inyo, California	37°17′	118°10′	2255	R	20 ii 78
183	M(8, 2)	Spring Mts, Kyle Canyon along Nev 157	Clark, Nevada	36°16′	115°36′	2105	B & Wa	2 iv 78
189	M(4, 6)	Sheep Range, Sawmill Canyon, Mormon Well Rd.	Clark, Nevada	36°42′	115°06′	1705	R	15 iv 78
190	M(2, 8)	Sheep Range, Sawmill Canyon	Clark, Nevada	36°41′	115°10′	2315	R	15 iv 78
191	M(6, 4)	Mormon Mts, Horse Spring	Lincoln, Nevada	36°56′	114°27′	1740	R	17 iv 78
213	M(7^{2}*, 1^{1}*)X(2)	Canyon Mts, 2·3 km E of Oak Creek Camp Ground	Millard, Utah	39°21′	112°14′	1950	B	11 ix 78
214	M(10, 0)	Snake Range, Lehman Creek Camp Ground	White Pine, Nevada	39°01′	114°15′	2350	B	12 ix 78
215	M(10, 0)	Sulphur Springs Range, Bruffey Canyon	Eureka, Nevada	40°13′	116°04′	1800	B & Ma	13 ix 78
216	M(10, 0)	Along US 93alt., 1·6 km W of Ferguson Springs Rest Area	Elko, Nevada	40°26′	114°12′	1935	B	27 ix 78
217	M(6, 4)	Deep Creek Mts, along Thomas Creek	Juab, Utah	39°52′	113°48′	1675	B	27 ix 78

218	M(3^{1}*, 3)E(1^{1}*)X(3)	1·6 km SSE of Swasey Peak	Millard, Utah	39°22′	113°18′	2285	B	29 ix 78
219	M(6^{1}*, 3^{1}*)X(1)	East Tintic Mts, 8 km W of Elberta	Utah, Utah	39°58′	112°02′	1740	B	30 ix 78
220	M(2^{1}*, 1)E(1)X(6)	West Tintic Mts, 1·6 km NNE of Lofgreen	Tooele, Utah	40°02′	112°18′	1745	B	30 ix 78
221	M(6, 4)	Northernmost Sheeprock Mts, 0·8 km SE of Lookout Pass	Tooele, Utah	40°07′	112°33′	1815	B	30 ix 78
225	M(9^{1}*, 1)	Grouse Creek Mts, 3 km N of Rocky Pass	Box Elder, Utah	41°33′	113°45′	2165	B	25 x 78
226	M(10, 0) TYPE locality	Masonic Mts, hills S side of Walker River valley	Mineral, Nevada	38°24′	119°07′	1950	B & R	29 x 78
227	M(10, 0)	Toquima Range, 3 km E of Manhattan	Nye, Nevada	38°33′	117°02′	2350	B & R	31 x 78
228	M(9, 1)	Shoshone Mts, Upper Silver Creek	Lander, Nevada	39°47′	117°13′	1860	B & R	31 x 78
229	M(10, 0)	Geiger Grade, along Nev 341, 3 km E of Steamboat Hot Springs	Washoe, Nevada	39°23′	119°43′	1525	B & R	2 xi 78
230	M(9, 1)	Toiyabe Range, Bob Scott Camp Ground, along US 50	Lander, Nevada	39°28′	117°00′	2165	B & R	2 xi 78
231	M(10, 0)	Paradise Mts, along Nev 844, E of Gabbs	Nye, Nevada	38°54′	117°51′	2090	B & R	2 xi 78
232	M(6, 2)F(2, 0)	Clark Mt, secondary summit ridge, c.1·6 km E of main summit ridge	San Bernardino, California	35°32′	115°35′	2380	B, R, & H	5 xi 78
233	M(2, 0)C(1, 4)F(3, 0)	Clark Mt, Picnic Ground on S side	San Bernardino, California	35°31′	115°35′	1830	B, R, & H	6 xi 78
234	M(9, 0)X(1)	Spring Mts, Potosí Pass	Clark, Nevada	35°59′	115°32′	1890	B, R, & H	6 xi 78
235	C(2, 0)F(8, 0)	Newberry Mts, Christmas Tree Pass	Clark, Nevada	35°16′	114°44′	1190	B, R, & H	7 xi 78
236	M(0, 1)C(3, 0)F(5, 0)X(1)	S end of McCullough Range, N of Nev 164	Clark, Nevada	35°32′	115°12′	1645	B, R, & H	7 xi 78
237	C(4^{1}*, 1)F(3, 0)X(2)	Northern New York Mts, nr. the Vanderbilt Mine	San Bernardino, California	35°19′	115°15′	1315	B, R, & H	8 xi 78
238	C(3^{1}*, 0)F(3^{1}*, 0)X(4)	New York Mts, above Keystone Canyon on sericite site	San Bernardino, California	35°16′	115°17′	1890	B, R, & H	8 xi 78
239	M(0, 1)C(2, 0)F(1^{1}*, 0)X(6)	New York Mts, above Keystone Canyon on limestone site	San Bernardino, California	35°16′	115°17′	1905	B, R, & H	8 xi 78
240	M(1, 1)C(3^{2}*, 1)F(3^{1}*, 1)	'Plateau' campsite on approach road to Keystone Canyon	San Bernardino, California	35°16′	115°16′	1585	B, R, & H	9 xi 78

APPENDIX—*continued*

Coll. No.	Determinations	Locality	County, State	Lat. (N)	Long. (W)	Elev. (m)	Collectors	Date
241	C(2, 2)F(3, 1)X(2)	Providence Mts, W end of Wild Horse Canyon	San Bernardino, California	35°03′	115°28′	1480	B, R, & H	9 xi 78
242	$C(9^{2*}, 1)$	Granite Mts, Cove Spring	San Bernardino, California	34°48′	115°38′	1265	B, R, & H	10 xi 78
243	C(8, 2)	Little San Bernardino Mts, Keys View, Joshua Tree Nat. Mon.	Riverside, California	33°56′	116°10′	1495	B, R, & H	11 xi 78
245	C(9, 1)	Pinyon Flat Camp Ground, along Cal 74	Riverside, California	33°35′	116°28′	1220	B, R, & H	12 xi 78
247	M(1, 1)X(8)	Lower Cushenbury Canyon, along Cal 18	San Bernardino, California	34°20′	116°50′	1525	B, R, & H	13 xi 78
249	$M(10^{1*}, 0)$	San Gabriel Mts, 5 km WNW of Big Pine	Los Angeles, California	34°24′	117°44′	1705	B, R, & H	15 xi 78
250	M(8, 2)	Coast Range, along Cal 33, Los Padres Nat. For.	Ventura, California	34°40′	119°22′	1310	B, R, & H	15 xi 78
251	M(10, 0)	Tehachapi Mts, Oak Creek Pass	Kern, California	35°03′	118°22′	1355	B, R, & H	16 xi 78
252	M(8, 2)	Sierra Nevada, 3 km NE of Farewell Gap	Inyo, California	36°29′	118°06′	2620	B, R, & H	16 xi 78
258	$M(0, 3^{1*})F(2^{2*}, 0)E(1)X(4)$	8 km S of Enterprise, along Ut 18	Washington, Utah	37°32′	113°39′	1875	B & Co	27 v 79
259	M(3, 7)	3·7 km W of Utah boundary, along Nev 319	Lincoln, Nevada	37°43′	114°06′	1820	B & Co	27 v 79
283	M(4, 5)X(1)	S corner of triangle at junction of US 6 and Ut 36	Juab, Utah	39°55′	112°09′	1845	B	23 ix 79
284	M(10, 0)	East Humboldt Mts, 40 km S of Wells	Elko, Nevada	40°46′	115°03′	1890	B	24 ix 79
285	M(9, 1)	Egan Range, 1·1 km W of Cherry Creek	White Pine, Nevada	39°54′	114°54′	1935	B	24 ix 79
286	$M(10^{1*}, 0)$	1·5 km S of Eureka, on ridge beside US 50	Eureka, Nevada	39°30′	115°58′	2045	B	24 ix 79
287	M(4, 1)C(0, 2)F(1, 0)X(2)	Kingston Range, 2·6 km WSW of Horse Thief Springs	San Bernardino, California	35°46′	115°55′	1800	B & R	3 x 79
288	$M(6, 2^{1*})C(1, 0)F(1, 0)$	Wilson Pass	Clark, Nevada	35°53′	115°31′	1525	B & R	3 x 79
289	$M(6^{1*}, 4)$	Spring Mts, below S end of Potosi Mt	Clark, Nevada	35°56′	115°30′	2010	B & R	3 x 79

290	C(6, 0)F(4, 0)	McCullough Range, McClanahan Spring	Clark, Nevada	35°40′	115°10′	1465	B & R	3 x 79
291	M(1, 0)F(9, 0)	Grapevine Wash, 1·2 km E of Diamond Bar Ranch headquarters	Mohave, Arizona	35°53′	113°58′	1340	B & R	5 x 79
292	C(9^{1}*, 0)F(1, 0)	Providence Mts, Mid Hills Camp Ground	San Bernardino, California	35°08′	115°26′	1700	B & R	6 x 79
294	C(7, 3)	Between I-8 and the Mexican border, 0·8 km SW of Smugglers Cave	Imperial, California	32°38′	116°06′	1190	B, R, & H	7 x 79
297	C(9, 0)X(1)	Sierra Juarez, 10 km SW of La Rumorosa	Tijuana, Baja California	32°28′	116°03′	1205	B, R, & H	8 x 79
301	C(2,1) (3 trees only)	5 km WSW of Cerro de la Cienega	Ensenada, Baja California	31°42′	115°51′	1295	B, R, & H	10 x 79
302	C(8, 2)	nr. San Matias Pass, S of BC 16	Ensenada, Baja California	31°17′	115°32′	1190	B, R, & H	11 x 79
305	C(9, 0)X(1)	c.midway between Mike's Sky Rancho and BC 16	Ensenada, Baja California	31°14′	115°36′	1190	B, R, & H	13 x 79
307	C(8,2)	E end of San Bernardino Mts, 5 km NW of Yucca Valley	San Bernardino, California	34°09′	116°28′	1190	B, R, & H	18 x 79
308	C(9, 0)F(1, 0)	Old Woman Mts, c.4 km W of Sunflower Spring	San Bernardino, California	34°32′	115°10′	1340	B & R	20 x 79
309	C(10, 0)	Providence Mts, 0·8 km W of Foshay Pass	San Bernardino, California	34°55′	115°33′	1280	B & R	21 x 79
310	M(9, 1)	Stillwater Range, 7 km NNE of Job Peak	Churchill, Nevada	39°38′	118°11′	1370	B	24 x 79
311	M(9^{2}*, 1)	Kawich Range, 4 km ESE of Peak	Nye, Nevada	37°57′	116°25′	2285	B	26 x 79
312	M(10, 0)	Timpahute Range, 4 km N of Coyote Peak	Lincoln, Nevada	37°40′	115°38′	1860	B	26 x 79
313	M(10^{1}*, 0)	Ely Range, Patterson Pass	Lincoln, Nevada	38°35′	114°43′	2255	B	27 x 79
314	M(8, 2)	Delamar Mts, Oak Spring Summit, along US 93	Lincoln, Nevada	37°36′	114°40′	1905	B	28 x 79
315	M(1, 1)E(3^{2}*)X(5)	Southern Wah Wah Mts	Beaver, Utah	38°11′	113°32′	2010	B	28 x 79
323	M(10^{1}*, 0)	Needle Range, 0·6 km N of Cougar Spar Mine	Beaver, Utah	38°13′	113°51′	2285	B	30 x 79
325	M(0, 1)E(3^{1}*)X(6)	3 km E of Pinto	Washington, Utah	37°33′	113°29′	1965	B	31 x 79

APPENDIX—*continued*

Coll. No.	Determinations	Locality	County, State	Lat. (N)	Long. (W)	Elev. (m)	Collectors	Date
326	M(6, 3)F(1, 0)	19·3 km W of Enterprise, Dixie Nat. For.	Iron, Utah	37°37′	113°56′	1800	B	31 x 79
327	M(7^1*, 1^1*)F(1, 0)X(1)	0·4 km E of south arm of Lower Enterprise Reservoir	Washington, Utah	37°32′	113°51′	1770	B	31 x 79
346	C(9, 1)	Coxcomb Range, N and NE slopes just below highest point of range	Riverside, California	34°02′	115°24′	1220	B & Wa	27 iv 80
352	M(2, 6^3*)X(2)	Canyon Mts, Leamington Pass	Millard, Utah	39°31′	112°12′	1815	B & Wa	1 v 80
361	M(9, 1)	Peavine Mt, NW slopes	Washoe, Nevada	39°37′	119°59′	1965	B & R	6 x 80
362	M(9, 1)	1·6 km N of Le Conte Point, Yosemite National Park	Tuolumne, California	37°58′	119°42′	1705	B & R	9 x 80
363	M(9^3*, 1)	Sierra Nevada, W slope, S end of Bear Ridge	Fresno, California	37°20′	118°59′	2165	B & R	11 x 80
364	M(8, 2)	Kings Canyon Nat. Park, along Copper Creek trail from canyon roadhead	Fresno, California	36°48′	118°35′	1740	B & R	12 x 80
365	M(10, 0)	Southern Sierra Nevada, Paiute Mt Road, Sequoia Nat. For.	Kern, California	35°25′	118°25′	1830	B, R, & N	13 x 80
366	M(9, 1)	Lockwood Valley Road, 1·4 km N of Chuchupate Ranger Station	Kern, California	34°49′	119°01′	1585	B, R, & N	13 x 80
368	M(9, 1)	San Gabriel Mts, c.3 km SW of Mt Emma	Los Angeles, California	34°27′	118°06′	1160	B & R	22 x 80
369	M(9, 1)	San Gabriel Mts, 11·3 km WNW of Cajon Pass	San Bernardino, California	34°23′	117°34′	1480	B & R	22 x 80
371	C(10, 0) TYPE locality	Vallecito Mts, NW base of Whale Peak, Anza-Borrego Desert State Park	San Diego, California	33°03′	116°20′	1280	B & R	25 x 80
373	M(10, 0)	Coast Range, 3 km N of Ortega Hill, along Cal 33	Ventura, California	34°36′	119°21′	1280	B & R	26 x 80
374	M(7, 3)	Coast Range, Santa Barbara Canyon, 3 km E of Fox Mt	Santa Barbara, California	34°49′	119°34′	945	B & R	26 x 80

375	M(8, 2)	Coso Range, NE slopes 0·5 km SW of Lower Centennial Spring	Inyo, California	36°16′	117°46′	1830	B & R	27 x 80
376	M(10, 0)	6·5 km by road WNW of Gold Hill	Tooele, Utah	40°12′	113°53′	1800	B	30 x 80
377	M(4, 4)X(2)	Northern Wasatch Mts, Dry Curtis Creek	Cache, Utah	41°36′	111°32′	1995	B & L	31 x 80
378	M(10, 0)	Hunter Mt, 0·8 km N of boundary of Death Valley Nat. Mon.	Inyo, California	36°33′	117°30′	2075	B	12 xi 80
384	C(7, 3)	Sierra la Asamblea	Ensenada, Baja California	29°17′	114°03′	1330	B & Wa	21 iii 81
397	M(10, 0)	Lone Mt, 3·1 km E of summit	Esmeralda, Nevada	38°02′	117°28′	2010	H & R	1 v 81
404	C(2, 0)F(7, 1)	Black Mts, 2·6 km N of Mt Nutt	Mohave, Arizona	35°07′	114°21′	1400	We	13 x 81
409	C(9, 1)	Sierra la Asamblea	Ensenada, Baja California	29°17′	114°03′	1330	B, R, & H	20 iii 82
411	C(4, 0)F(6, 0)	Newberry Mts, Christmas Tree Pass	Clark, Nevada	35°16′	114°44′	1160	B & Wa	29 iii 82
428	M(10, 0)	White Mts, NE face of Black Mtn.	Inyo, California	37°16′	118°13′	2715	H & R	19 xi 83
429 (1)	M(10, 0)	Inyo Range, Andrews Mt, N to NW slopes near summit	Inyo, California	37°05′	118°05′	2865	H & R	10 ii 84
429 (2)	M(7, 0) (7 trees only)	Inyo Range, Andrews Mt, N to NW slopes including summit	Inyo, California	37°05′	118°05′	2870	H & R	10 ii 84
438	E(5)X(5)	New York Mts, along crest at head of 'Fir Canyon'	San Bernardino, California	35°16′	115°19′	2210	B, R, H & C	16 x 84
439	F(1^{1}*, 0)X(9)	New York Mts, just W of Keystone Mine (now Copper Queen #2)	San Bernardino, California	35°16′	115°18′	1950	B & C	16 x 84
440	M(8, 2)	5 km NNW of Pioche, just W of mine on lower N slope of Mt Ely	Lincoln, Nevada	37°57′	114°30′	1845	B, R, H & C	17 x 84
443	C(1, 0)X(1) (2 trees only)	Spring Mts, Red Rocks Canyon Nat. Rec. Area, Willow Spring Picnic Area	Clark, Nevada	36°10′	115°30′	1390	B	21 xi 84
447	M(0, 4^{1}*)C(1, 0)F(3, 0)X(2)	same as collection 443	Clark, Nevada	36°10′	115°30′	1390	B	4 iv 85
448	M(10, 0)	Lone Mt, area of lesser summit	Esmeralda, Nevada	38°01′	117°30′	2550	H & R	26 iv 85
450	M(6, 4)	Keg Mts, 0·3 km W of Willow Springs water tank	Juab, Utah	39°49′	112°50′	1770	B	27 ix 85
451	M(9, 1)	Burbank Hills, Juniper Pass	Millard, Utah	38°51′	113°52′	2040	B	29 ix 85

APPENDIX—*continued*

Coll. No.	Determinations	Locality	County, State	Lat. (N)	Long. (W)	Elev. (m)	Collectors	Date
452	M(6, 2)X(2)	Crystal Peak, along road at N base	Millard, Utah	38°48′	113°36′	1890	B	29 ix 85
453	M(1^{1}*, 0)E(5)X(4)	Pavant Range, N end, 0·4 km E of Scipio Pass	Millard, Utah	39°12′	112°10′	1855	B	30 ix 85
454	M(1, 0)E(4)X(5)	Valley Mts, NE end, 8 km NNE of Scipio	Juab, Utah	39°19′	112°04′	1720	B	30 ix 85
457	M(2, 0)C(3, 0)F(2^{1}*, 0)X(3)	Between New York Mts and Mid Hills, Howe Spring	San Bernardino, California	35°13′	115°22′	1730	B & R	20 x 85
458	C(9, 0)F(1, 0)	Providence Mts, 2·4 km N of Bonanza King Mine	San Bernardino, California	35°00′	115°30′	1430	B & R	21 x 85
459	C(7, 2)X(1)	Little San Bernardino Mts, 0·5 km S of Eureka Mt, Joshua Tree Nat. Mon.	Riverside, California	34°02′	116°21′	1640	B & R	22 x 85
460	M(3, 0)C(6, 0)X(1)	Eastern San Bernardino Mts, c.1·9 km ENE of Tip Top Mt summit	San Bernardino, California	34°16′	116°40′	1710	B & R	23 x 85
461	C(5, 5)	Eagle Mt, N slopes, Joshua Tree Nat. Mon.	Riverside, California	33°46′	115°45′	1100	B & R	24 x 85
462	C(6, 4)	Vallecito Mts, summit area of Whale Peak, Anza-Borrego Desert State Park	San Diego, California	33°02′	116°19′	1630	B & R	26 x 85
463	C(5, 5)	Vallecito Mts, lowest specimens, along S side of Pinyon Mt Valley, 4 km NW of Whale Peak summit, Anza-Borrego Desert State Park	San Diego, California	33°03′	116°21′	1110	B & R	27 x 85
464	M(0, 1)F(8, 1)	Virgin Mts, along Elbow Canyon Road	Mohave, Arizona	36°46′	113°54′	1435	B & R	28 x 85

COLLECTORS and those assisting: *B*, D. K. Bailey; *C*, A. J. Corner; *Co*, J. K. Corner; *G*, J. F. Griggs Jr.; *H*, W. E. Horn; *L*, R. M. Lanner; *Ma*, R. J. Mastrogiuseppe; *Mi*, B. Miller; *N*, D. Norris; *P*, A. Peacock; *R*, E. C. Rockwell Jr.; *Sn*, K. Snajberk; *Su*, K. W. Sullivan; *Wa*, J. M. Watts; *We*, G. W. Welsh; *Z*, E. Zavarin.

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