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TAXONOMY, SYSTEMATICS, AND PHYLOGENY OF *PINUS*, SUBSECTION *PONDEROSAE* LOUDON (*PINACEAE*). ALTERNATIVE CONCEPTS

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Abstract: Whoever attempts to revise *Pinus ponderosa* and its complex will soon be faced with a diversity of inconsistencies between the vast amount of data already available on the group and its present taxonomic arrangement. By and by it becomes apparent that a variety of profound misconceptions deeply rooted in the minds of modern researchers in this particular field is responsible for the fact that the pattern of variability and diversity is still poorly understood in *Pinus ponderosa*, in the *Ponderosa*—complex, and in the *Ponderosae* in general. All these misconceptions must be virtually refuted once and for all before a taxonomic revision can at all be successfully ventured. These pages aim at discussing alternative concepts probably better explaining the variability and diversity exhibited by the yellow pines. The misconceptions proposed to be refuted include the erroneous notion that *Pinus ponderosa* sensu lato is of southern (Madro Tertiary) origin, and is, at present, experiencing evolutive processes and adaptive radiation, or hybridizing, e.g. with *Pinus washoensis*. Contrary to widespread belief it is suggested that *Ponderosae*, *Australes*, and *Sabinianae* are of common origin and more closely related to one another, and that this large group ought not to be subdivided according to geography alone, but ought to be seen in the context of the general Cenozoic history of North American vegetation; and that *Pinus ponderosa* s.l. is, in fact, the veritable key to a proper understanding of diversity, phylogeny, and Tertiary biogeography of all the yellow pines of North America in general. It will then become clear that the large yellow pine-group probably consists of a variety of distinct phylads which have themselves become geographically disjunct during the Tertiary, in a pattern similar to that already recognized as the *Pinus strobus - P. monticola - P. strobus* var. *chiapensis*-phylad; that the disjunct, related components of these yellow pine phylads are at present hidden among *Australes* in the East, the *Ponderosa*-complex in the West, and the *Montezuma*- and *Pseudostrobus*-complexes in Mexico, complexes which, in their present circumscription, will probably prove to be mere artificial groups; it will also become apparent that this pattern of diversity of yellow pine-phylads of Early Tertiary age is superimposed by a pattern consisting of primary, and secondary Middle, and Later Tertiary vicariads originating from these Early Tertiary ancestor-taxa. Immature female cone colour probably is the proper characteristic to distinguish between ancestors and their vicariads in the *Ponderosae* (in *Pinus* and the *Pinaceae* in general). It is further suggested that all the "heptane pines" among *Sabinianae* and other yellow pines constitute a coherent, independent phylad, although related to the other yellow pines, and that the Sierra Nevada western slope *Ponderosa* pine, of Pliocene origin, erroneously considered to be the "archetype" of *Pinus ponderosa*, may only be the genetically already distant, youngest phylogenetic offspring of *Pinus ponderosa* s.l., and may thus have deluded geneticists into wrong conclusions as to the relationship of this "race" to other yellow pines. Finally, putative complementary diagnostic characters in the *Ponderosae*, and the probable significance of immature female cone colour to taxonomy and to phylogenetic reconstruction in the *Ponderosae* (in *Pinus* in general) are discussed. Detailed taxonomic, and nomenclatoral considerations are deliberately avoided, since they would probably be premature at present, but the formulation of a taxonomic concept applicable to the *Ponderosae* is attempted.

Introduction

All former and present researchers in the yellow pines of the western United States and Mexico unisono point out the great diversity and tremendous morphological variability exhibited by these pines; one of the consequences of these circumstances is that the taxonomists among them, in spite of a multitude of attempts, have in fact failed so far to convincingly delimit species boundaries between taxa, and to achieve an undisputed classification of this array of diversity. Though much data towards a better knowledge of the yellow pines has accumulated in the recent past, the opinion of taxonomists still stretches from extreme taxonomic diversity in the *Ponderosae*, to extreme variability in a few species (KRÜSSMANN G., 1983; MARTINEZ M., 1948; MIROV N.T., 1967; SHAW G.R., 1914; SILBA J., 1984, and 1986; STEAD J.W., 1983; STEAD J.W. & STYLES B.T., 1984); in the *Ponderosa*-complex presumed more or less broad clinal morphological variation, adaptive radiation, and more or less high levels of hybridization between "races" and/or taxa, are contrasted by a broad array of controversial and inconsistent evidence partly to the contrary (AXELROD D.I., 1986, p. 587-590; CONKLE M.T. & CRITCHFIELD W.B., 1988; CRITCHFIELD W.B., 1984; HALLER J.R., 1962, 1965, 1984, and 1987; KUNG F.H. & WRIGHT J.W., 1972).

Among the western yellow pines an enormous amount of literature, and data, has accumulated up to the present on *Pinus ponderosa* alone. Still, its taxonomy is more controversial than ever and far from being convincingly settled. This conviction is one outgrowth of more than a decade of attachment to the subject. It appears that true complexity of the problem, but also neglect of substantial parts of the data and misinterpretation of still other parts is largely responsible for the steadfast adherence of taxonomists to obvious misconceptions never likely to result in a universally accepted taxonomy of *Pinus ponderosa* sensu lato. These misconceptions, on the contrary, only have resulted in a chaotic nomenclature and synonymy in the *Ponderosae*, but also in the *Ponderosa*-complex, the latter about to be indexed in a separate paper. However, since *Pinus ponderosa*, or whatever today is considered to be included in it, is the key "taxon" for a proper understanding of diversity, phylogeny, and historical biogeography of the *Ponderosae* as a whole, and a proper understanding of these topics is likely to substantially contribute to the achievement of a clearer systematic arrangement of the genus *Pinus* in general, it is indispensable to refute once and for all the misconceptions pertaining to these topics, before the task of revising the *Ponderosa*-complex (as begun by the present author), or the Mexican *Ponderosae*, can at all be successfully ventured. The following sentences aim to furnish an introductory outline of the nature of these misconceptions:

Many species of the genus *Pinus* are endowed with a truly variable genome expressed in tremendous phenotypic plasticity, and responsible for their evolutionary and ecological success (paleobotanical history probably explains readily lacking plasticity in other species). *Pinus ponderosa* s.l. is no exception. *Pinus*, on the other hand, is a very old and, moreover, very conservative genus (PRAGER E.M. & al., 1976), seed-cones (MILLER C.N., Jr., 1977), and pollen-grains (MILLAY M.A. & al., 1976) of which have not substantially evolved structurally since Early, and fascicles of needles at least since Upper Cretaceous (STOCKEY R.A. & al., 1986). But, extreme variability in a few conspicuously complex (and probably only poorly understood) groups of pines has been interpreted as an active evolutive process (e.g. *Ponderosae* in Mexico, see MIROV N.T., 1967). *Pinus ponderosa* sensu lato is a smaller, quite demonstrative example within the much larger group *Ponderosae*. Some authors (e.g. HALLER J.R., 1965, 1984, and 1987) have time and again attempted to explain its variability as being the action of adaptive radiation, and in a rather small part of its geographic range (e.g. Pacific Northwest, and including *Pinus washoensis*) as originating from hybridization (hybrid swarms) and a similar evolutive process active at present. However, the Pacific Northwest, according to all other evidence, rather more or less is the remnant territory of an earlier much more ubiquitous distribution of species of pine (conifers in general), and a general area of retreat for many arborescent species that were much more widespread during the Tertiary, when climate was more favorable (AXELROD D.I., 1958, 1976, 1986, and 1988; DAUBENMIRE R., 1978, etc. ...). All paleobotanical and biogeographic evidence points to a much more widespread occurrence of *Pinus* cf. *ponderosa* during earlier Tertiary (AXELROD D.I., 1986 and references cited therein). Those genotype(s) of *Pinus ponderosa* sensu lato from the Pacific Northwest (as meant by HALLER J.R., 1984, 1987, and characterized more in detail by CONKLE M.T. & al., 1988, and CRITCHFIELD W.B., 1984) obviously have retreated into this refugium of relative equability of climate, and are neither thriving in their "optimum", nor surviving in a generally critical state, although declining at the harsh eastern edge of the area (AXELROD D.I., 1986), indicating that the range of adaptation of the particular genotype is expiring, and that opportunities furnished by new, dryer habitats becoming available in the area (founder effect), cannot be exploitet anymore. Paleospecies of plants in general (including conifers) habing lived in this area in Miocene time, some 12 Ma ago, are generally indistinguishable from species now living in the Pacific Northwest (AXELROD D.I., 1976, p.14 and 24). All these circumstances at least cast profound doubt on the postulate of present variability being an expression of active evolutive processes. 1 to 2 Ma of Pleistocene and Holocene climatic fluctuations appear to have been far too short an interval (especially the relatively very short interglacials which are thought to have lasted for about 7000 to 15000 years only, as compared to the 60000 to 90000 years for the corresponding full glacials; data reviewed by SPAULDING W.G., 1984, p.43), with types of pressures apparently not properly effective to enhance macroevolutionary changes (as compared to migration, see HUNTLEY B. & al., 1989; SPAULDING W.G., 1984, p.63;) in a generally conservative long-lived woody conifer taxon like *Pinus ponderosa*, of which, in such widely separated areas profoundly affected by Pleistocene climatic fluctuations (British Columbia, Nebraska, California, New Mexico, etc. ...), only three varietal taxa of *Ponderosa* pine are scarcely, and controversially accepted at present. Evolutive processes may have been effective at the onset of the Pleistocene (SPAULDING W.G., 1984), but evidence for coinciding macroevolutionary change is generally absent (HUNTLEY B. & al., 1989): "..... The trees of today are adapted to both glacial and interglacial climates, and to the climatic change that occurs at the transition ....." (SPAULDING W.G., 1984).

Present time adaptive radiation is postulated to be another explanation for variation, especially in needle-number, in *Pinus ponderosa* sensu lato in different ecogeographic regions (HALLER J.R., 1987). However, this assumption is also strongly contradicted by the general paleohistory of North American vegetation (as convincingly outlined by D.I. AXELROD 1958, 1976, 1986 and 1988, DAUBENMIRE R. 1978, and other workers), which implies that contacts between the "variants in needle-number" (varieties scopulorum and arizonica) and their ancestors must have been interrupted since practically Middle Tertiary time (see also KUNG F.H. & al., 1972). Opportunities for *Pinus* in general, and *Pinus ponderosa* sensu lato in particular (old genus and old species!), to continually evolve into more and more specialised habitats have, contrary to the criticized view, generally been more and more restricted (with perhaps one particular exception not involving the "variants in needle number", see paragraph No 4) since Oligocene time. *Pinus ponderosa* sensu lato better tolerates dryness than most other arborescent species in the West. But, a slightly modified attitude towards xerophytic adaptation in this taxon must be adopted since "variants in needle-number" of *Pinus ponderosa* sensu lato have, actually, not evolved into habitats ever becoming dryer (practically all kinds of habitats have more and more become dryer since Middle Tertiary time), but are now, to the contrary, restricted to areas where, at least, the particular minimum of summer precipitation required by the genome of *Pinus ponderosa* sensu lato is still available. The "archetype", Sierra Nevada western slope *Ponderosa* pine in the West, must cope with precipitation less evenly distributed throughout the year than its "variants" in the East. The sharp ecological differences among "races" of *Pinus ponderosa* s.l. are also strong evidence, therefore, against affiliating the *Ponderosa*-complex with the xerophytic Madro-Tertiary Geoflora. Restriction of its larger area of distribution in earlier Tertiary gradually occurred from East to West. Adaptive radiation from West to East was and is, therefore, out of the question. Other causes must account for the (also much earlier) origin of ecogeographical differences in needle-number in *Pinus ponderosa* s.l.

Clinal morphological variation in *Pinus ponderosa* sensu lato (including *Pinus washoensis*) on an altitudinal gradient from northeastern California into southwestern Oregon has been interpreted as hybridization (hybrid swarms) occuring between Sierra Nevada western slope *Ponderosa* pine and *Pinus washoensis* (or, better, *Pinus ponderosa* sensu lato) farther to the North (HALLER J.R., 1965, 1984, 1987), although the nature of the evidence on which such a statement is based is not presented (probably based uniquely on reports of variation in immature female cone colour as reported by R.H. SMITH, 1981; see probable explanation of this phenomenon in paragraph No 5). Hybridization (especially a hybrid swarm), on the other hand, is rendered strongly improbable by results of hybridization experiments (CRITCHFIELD W.B., 1984, p.163) which have shown Sierra Nevada western slope *Ponderosa* pine to be but distantly related to North Plateau "races" of *Pinus ponderosa* sensu lato, and to *Pinus washoensis*. The low crossability shown by these experiments indicates that low level hybridization may actually occur in the area, but also, that introgression, and hybrid swarms, are not likely to exist. The variants along and on both ends of the gradient are, moreover, practically not differentiated biochemically (SMITH R.H., 1981). It is more likely that "races" of *Pinus ponderosa* sensu lato on the North Plateau, and Sierra Nevada western slope *Ponderosa* pine do, acutally, maintain a genetic integrity similar to that existing among other sympatric genotypes of the *Ponderosa*-complex. Again, other explanations must exist for variability and diversity exhibited in this region of contact (see paragraph No 5). Diversity in *Pinus ponderosa* s.l., admittedly, is very complex, and the extent to which the thesis of "variation" appears to emanate solely from an inadequate understanding of this diversity, is perhaps best exemplified by the following array of tentative conclusions, as reached by one and the same author in several years of truly thorough research in the *Ponderosa*-complex:

"The status of (*Pinus washoensis*) as a species seems questionable" (HALLER J.R., 1965); "Washoe pine may have at least reached the point of incipient speciation" (HALLER J.R., 1984); "*Pinus washoensis* (is) possibly disappearing as a distinct entity" (HALLER J.R., 1987).

If, however, all data available for *Pinus ponderosa* sensu lato is set into the frame of the Cenozoic general history of North American vegetation (as done in the following paragraphs), a much more consistent picture at once emerges. Present time discernible evolutive processes in *Pinus ponderosa* in this area, or adaptive radiation, or hybrid swarms, appear, consequently, to be but a very remote possibility, or even less likely, and the perpetuation of such an opinion to be one of the pitfalls probably obstructing insights towards more convincing results. As long as conclusive evidence in favour of the criticized postulates cannot be presented, solutions to the problems of obvious variability and presumed introgression within and among "races" of *Pinus ponderosa* s.l. of the Pacific Northwest ought also to be sought elsewhere, and these features are, perhaps, more parsimoniously explained by the (probable) paleohistory of the *Ponderosa*-complex and/or its diversity may, perhaps, more convincingly be systematized with the aid of a taxonomic concept more consistent with this historical topic. Phenotypic plasticity, no doubt, is a common feature also exhibited by the genome(s) of *Pinus ponderosa* sensu lato. However, the sum of data present on this complex contains by far too great an amount of inconsistencies and contradictory evidence, indicating that the present boundaries between taxa probably are not natural delimitations. The haze hiding natural subdivisions must be dissipated prior to more detailed revisionary work.

Several similarly foundamental pitfalls (concerning the geographic origin of the *Ponderosae*; the relationship of *Australes* and *Ponderosae*; the phylogenetic sequence of origin of the component members of the *Ponderosae*) appear to have largely blurred the true significance of facts, and how they interfinger. These pitfalls must be eliminated to make the otherwise obvious significance apparent. I aim at persuading that, instead of maintaining unsuccessful ideas, new lines of thought or alternative concepts (taxonomic and others) ought to be tested until convincing results supported by all available evidence are achieved in the *Ponderosae*. But, since antecedent supplementing of the vast amount of data already available appears to be crucial in many instances before better results can be obtained, *the present alternative concepts do not yet in themselves substitute* the anticipated solutions to the problems in *Pinus ponderosa* taxonomy, but rather represent the indispensable new point of departure and an indication of the direction into which more detailed investigations ought to be conducted.

The discussion in the previously cited references of several "races" of *Pinus ponderosa* (Pacific Northwest or North Plateau, Sierra Nevada, Coast Ranges, Transverse Ranges, etc. ...), and their admittedly poorly understood interrelationships may, moreover, serve as an introductory glimpse at the taxonomic and nomenclatoral (synonymy!) chaos at present met with in *Pinus ponderosa* sensu lato (and the *Ponderosae* in general). Among the three species-complexes (sensu MIROV N.T., 1967, p.558) composing *Pinus* L., subsection *Ponderosae* LOUDON (sensu LITTLE E.L., Jr. & CRITCHFIELD W.B., 1969), general taxonomic considerations in this paper are (for the sake of clarity) in the main restricted to the six taxa of the *Ponderosa*-complex in their present circumscription (nomenclatoral considerations have not even been attempted here): *Pinus ponderosa* DOUGLAS ex LAWSON, its varieties scopulorum ENGELMANN and arizonica (ENGELMANN) SHAW, *Pinus jeffreyi* GREVILLE & BALFOUR, *P. washoensis* MASON & STOCKWELL, and *P. engelmannii* CARRIERE. However, in elaborating considerations of their systematics and phylogeny, it is necessary to include, as well, in a more or less general way the complexes of *Ponderosae* in Mexico (similarly in their present circumscription), and the pines of subsection *Australes* (LOUDON) LITTLE & CRITCHFIELD (1969).

The "Pacific Northwest", or "North Plateau" race(s) of *Pinus ponderosa* is the source of so much and so profound a confusion (including the taxon called *Pinus washoensis*), in itself, and in connection with Sierra Nevada western slope *Ponderosa* pine, that these "races" are kept distinct wherever necessary in this manuscript, and the Pacific Northwest, or North

Plateau race is always termed "*Pinus ponderosa* sensu lato of the Northwest". It is an admitted fact that Sierra Nevada western slope *Ponderosa* pine thrives in a summer-dry climate, while *Pinus ponderosa* sensu lato of the Pacific Northwest enjoys a summer-wet regime (e.g. CONKLE M.T. & al., 1988, etc.). In spite of these profound ecological differences, among other ecological, morphological, biochemical, and genealogical evidence, the two (or more) "races" are still classed as one single taxon. The controversy on the geographic origin of *Pinus ponderosa* as a whole perhaps also illustrates that *Pinus ponderosa* sensu lato of the Pacific Northwest appears yet not to have been adequately surveyed botanically, and that this "race" and Sierra Nevada western slope *Ponderosa* pine, in fact represent entirely different things, actually entities too different in several respects, and the northern race itself too incoherent a group, to be termed "races" of only a single taxon.

Paleontological setting

The genus *Pinus* is believed to have originated in eastern Asia and to have migrated into North America via Beringia (MIROV N.T., 1967, p.116-117, 573). The members of the genus were widespread on the American continent and had reached present Mexico by early Tertiary (FLORIN R., 1963, p.254; MIROV N.T., 1967, p.116-117, 574) or even earlier (AXELROD D.I., 1988, p.305; RZEDOWSKI J., 1978, p.91) along uplands and on somewhat drier sites. Climate then was quite warmer and more equable than today, with ample precipitation more evenly distributed throughout the year (AXELROD D.I., 1976, p.2; AXELROD D.I., 1986, p.599), although more or less pronounced dry seasons have existed (MIROV N.T., 1967). Much like in modern times the plant species of the Tertiary occupied particular habitats and were restricted altitudinally to the particular, and distinct vegetation or forest zone (montane conifer, mixed conifer, woodland, etc. ...) they were adapted for (AXELROD D.I. 1988). Particular habitats, however, due to the general equability of climate, were of smaller extent, although widespread across the continent; forest zones were far less pronounced than today, and generally intergrading into one another (AXELROD D.I., 1988). Although pines seem to have been ubiquitous as groves, they as well seem to have been much less numerous in individuals and a less conspicuous floral element than at present (MIROV N.T., 1967, p.41, 116).

The probable small size of populations of any species (of *Pinus*), coupled with vast Early Tertiary ecological opportunities (demise of the Mesozoic plant-world, Laramide orogeny, etc.), a North to South and West to East general direction of migration (MIROV N.T., 1967, p.38, 52), and the resulting particular pattern of widespread distribution emphasized above, have undoubtedly favoured speciation and the sort of stepping-stone pattern of diversity as encountered in some modern groups within the genus *Pinus* in western North America today. Evolution of these early Tertiary phyletic lines has probably slowed down in Later Eocene/Early Oligocene. Some authors consider modern species of pine of the Cordilleran axis (from where the older lineages by then already were receding to the West and East) to generally correspond in their morphological features to their ancestors of the Oligocene (AXELROD D.I. & RAVEN P.H., 1985, p.30, 38), and on the Pacific Slope (where the older lineages persisted) to their ancestors of the Miocene (AXELROD D.I., 1976, p.14, 24).

Depending on the place of origin of early Tertiary ancestors of recent elements composing the flora of North America, several workers now distinguish between descendents of either the Neotropical-Tertiary, or the Arcto-Tertiary Geoflora (AXELROD D.I., 1958). These Geofloras met at middle latitudes on the continent forming a rather very broad transitional zone that approximately encompassed the conterminous United States (the broad ecotone of DAUBENMIRE R., 1978, p.53). With the onset in the Oligocene of the cooling and drying trend, and the more and more pronounced seasonality already alluded to, there evolved from preadapted elements of the local flora then present in what now is southwestern United States and northern Mexico, the conspicuously xerophytic Madro-Tertiary Geoflora (AXELROD D.I., 1958). The cooling trend was to culminate in the glacial periods of the Pleistocene at the onset of the Quaternary.

Elements of the Neotropical-Tertiary Geoflora more and more receded to the South opening areas to be invaded by elements of the Arcto-Tertiary Geoflora or elements evolving with the Madro-Tertiary Geoflora. Apart from glacial and interglacial, or other climatic fluctuations in the Neogene, the later Tertiary general direction of migration for members of both, the Arcto-, and the Neotropical-Tertiary Geofloras was, therefore, from North to South. The drying trend, coupled with major orogenic events all during the Pliocene (uplifting of the Sierra Nevada, the Cascades, the Rocky Mountains, and the Colorado Plateau), and the rainshadows formed by these events were to result in the arid Interior West of the United

States (AXELROD D.I., 1976, p.17; DAUBENMIRE R., 1978, p.58). Dryer conditions forced a midcontinental arid tract from the Gulf of Mexico northward, thus splitting into eastern and western (or even more) segments former continuous areas of distribution of plant species composing the mesophytic element of the Arcto-Tertiary Geoflora (DAUBENMIRE R., 1978, p.119). In this very publication (p.144, 166) are listed several taxa of plants whose present occurrence vividly reflects more widespread distribution in Early Tertiary. Among these taxa is also listed the mesophytic *Pinus strobus* which, like practically all members of the genus *Pinus* has migrated from the North and, therefore, is of Arcto-Tertiary origin. *Pinus strobus* has its well known recent occurrence in eastern North America. It's Tertiary populations in western North America, as a consequence of the climatic changes mentioned above, have since become disjunct and have, moreover, evolved into the slightly distinct *Pinus monticola*; and thousands of kilometers away in southern Mexico a taxon almost indistinguishable from the northeastern *Pinus strobus* (*Pinus strobus* , var. *chiapensis*) has survived to the present (AXELROD D.I., 1986, p.573, text-figure 5; DAUBENMIRE R., 1978, p.165). The modern conifer-phylads *Pinus banksiana* / *P. contorta*, and *Abies balsamea* and *A. fraseri* / *A. lasiocarpa* and *A. lasiocarpa* var. *arizonica* , among others, seemingly represent additional, more or less vivid instances for a similar Tertiary history.

Contrary to the general direction of migration for the elements of the two other Geofloras, the members of the Madro-Tertiary Geoflora, along with the northward movement of aridity, radiated into several directions and migrated, therefore, also to the North.

As a consequence of these climatic changes, western North America, and particularly the "Pacific Northwest", became a refuge for many arborescent taxa that were more widespread in earlier Tertiary, when their requirements for more equability of climate, and a substantial amount of precipitation during summer could also be met with in the Interior to the East (AXELROD D.I., 1986, and 1988).

Several workers indicate the occurrence of a pronounced climatic deterioration at the Eocene/Oligocene boundary, a "terminal Eocene event" (e.g. WOLFE J.A., 1978). Other authors (e.g. AXELROD D.I., 1987, p.65), although postulating a more gradual deterioration, have termed it the "Oligocene Crisis". However pronounced this Oligocene climatic deterioration may have been, it appears to have been quite a strong forcing factor to trigger evolutionary change on a holarctic scale in a conspicuous external, but ephemeral feature (immature cone colour) of the conservative genus *Pinus*, and probably of the *Pinaceae* in general. Beginning continentality of climate (wider range of temperature extremes, rather than a significant drop in overall mean temperature), appears to have been the nature of the forcing factor accounting for this evolutionary response of *Pinus* (and *Pinaceae*) in Middle Tertiary time.

Alternative concepts

1) Geographic origin and antiquity of the *Ponderosa*-complex

The present center of diversity of any taxon universally is considered to also be its place of origin. Other workers, however sustaining the general hypothesis, nevertheless emphasize the importance of including into these considerations the paleobotanical history of the particular taxon, and of available climatic and geologic data (AXELROD D.I., 1958, p.437). Cretaceous members of the genus *Pinus* have migrated and spread over North America from the North in early Tertiary (MIROV N.T., 1967, p.38, 52). Only xerophytes are thought to have migrated with other members of the Madro-Tertiary Geoflora also to the North in later Tertiary (AXELROD D.I., 1958), and several workers consider *Pinus ponderosa* to be a xerophyte.

These several and in certain cases seemingly contradicting general and particular hypotheses have brought about a broad array of opinions concerning the geographic origin of the *Ponderosae* in general and the more or less xerophytic *Ponderosa*-complex in particular:

Workers, who put emphasis on the general migratory trend in *Pinus*, always have insisted on the North as the geographic origin of the *Ponderosae* in general (e.g. MIROV N.T., 1967, who, however, considers the highlands of Mexico to be a secondary evolutionary center (p.343-346); FLORIN R., 1963, p.254, on the contrary, pleads for the hypothesis of a secondary North to South migration of *Pinus* in Pliocene/Pleistocene time). Workers, who put emphasis on xerophytic behaviour, firmly consider *Pinus ponderosa* sensu lato to be of Madro-Tertiary origin (DAUBENMIRE R., 1978, p.168; DETLING L.R., 1968). Still other workers, although the results of their researches do, in fact, point to the necessity of a different view, seem to be prevented by the present, perseveringly confusing taxonomy of *Pinus ponderosa* sensu lato to convert these results into new general lines of thought (AXELROD D.I., 1986, especially p.587-590).

None of these hypotheses seems to be true as a whole. All available evidence points, in fact, to a northern origin of the pines of the *Ponderosa*-complex and with them of all *Ponderosae*. Several *Ponderosae* are typically mesophytic (e.g. *Pinus pseudostrobus*) and if one considers *Pinus ponderosa* to be a xerophyte, a view that may have somehow concealed the related facts (e.g. the necessity of summer precipitation, as required by almost all its genotypes), it has to be kept in mind that plants adapted to dry conditions have, after all, not only evolved with the Madro-Tertiary Geoflora. Some of them, preadapted to dryness and now native to the dry northwestern interior, obviously were of Arcto-Tertiary origin (for examples see DAUBENMIRE R., 1978, p.195, 204). It is necessary to adopt a somewhat different attitude towards the concept of "xerophytism" in *Pinus ponderosa* sensu lato (see "Introduction").

It has generally remained unnoticed that several workers have reported in the recent past of finds of petrified cones and other macrofossils from Eocene and Oligocene strata in northwestern United States, in British Columbia, and elsewhere (Mississippi, Maryland), which after examination of their anatomical structure, though of close affinity to the yellow pines, cannot definitely be assigned to either the (recent) *Australes* or to the (recent) *Ponderosae* (BLACKWELL W.H., 1984; MILLER C.N., 1969; STOCKEY R.A., 1983; STOCKEY R.A., 1984; UNDERWOOD J.C. & MILLER C.N., 1980; also MILLER C.N. & MALINSKY J.M., 1986; some of these papers were well recorded by D.I. AXELROD, 1986, p.585, although, amazingly, not interpreted at all).

These finds, if interpreted adequately, (besides implying a closer relationship between *Australes* and *Ponderosae* than accepted at present, see subsequent paragraph) would quite clearly confirm the northern origin of the common group *Australes*/*Ponderosae*, explain the widespread Tertiary occurrence of *Pinus* cf. *ponderosa*, and confirm the present status of *Pinus washoensis* as a relict on eastern slopes of the Sierra Nevada (or in the "Pacific Northwest" or "North Plateau Region" in general) so much wondered at (AXELROD D.I., 1986, p.587-590), the antiquity of *Pinus ponderosa* in the Intermountain Region (AXELROD D.I., 1986, p.585,

586) and on the "North Plateau" (CRITCHFIELD W.B., 1984, p.167), and the long separation of the Pacific Slope-Ponderosa pine from its Rocky Mountain-relatives (KUNG F.H. & WRIGHT J.W., 1972, p.84). The probable relations of these older lines to the relatively younger lines of descent in the Rocky Mountains and in the Sierra Nevada are discussed in the following paragraphs.

I consider the *Ponderosae* to clearly be of northern affinity, very likely having had their center of diversification in the "Pacific Northwest", the Northern Rocky Mountains and, perhaps, in the present "Intermountain Region", and having spread southward, and eastward from there in early Tertiary. More arguments to sustain this hypothesis are discussed in the following paragrphs; and although *still more evidence certainly is* hidden in Mexico, it is beyond the scope of this paper to also deal in detail with the complexes of yellow pines there. It is interesting to note, however, that *Pinus hartwegii* , for instance, (worldwide the only pine to reach altitudes of as much as 4000 m) and its floristic community is described as belonging to the subalpine forest-zone and the ground cover under its canopy to clearly be of Arcto-Tertiary origin (DAUBENMIRE R., 1978, p.117).

In a recent paper, CONKLE M.T. & CRITCHFIELD W.B. (1988) have tentatively proposed a somewhat modified hypothesis derived from the ill-fated concept of a southern origin of the *Ponderosae*: From the general absence of macrofossils of *Pinus* cf. *ponderosa* in the Pacific Northwest younger than Miocene and, similarly, from remains in packrat middens in the Southwest of late glacial, Wisconsin age, they conclude that *Pinus ponderosa* sensu lato, including all its varieties, is itself only a Holocene immigrant from the South having migrated northward along the west coast (var. *ponderosa*) and along some interior mountain axis (var. *scopulorum*) during the present warm postglacial interval.

Such a sequence of events appears, practically, to be out of the question. If it were true, one would expect *Pinus ponderosa* of the "Pacific Slope" to be a high montane species in southern California gradually occupying lower elevations to the northern limit of its range. But, the opposite, actually, is the case. Sierra Nevada western slope *Ponderosa* pine occurs at elevations from 100 to 2300 m, but usually no higher than lower montane forest (HALLER J.R., 1984). Farther to the North *Pinus ponderosa* sensu lato (the morphologically, and ecologically (summer-wet) so much different "race", which contrary to all rational reasoning is still considered to be the very same taxon than the summer-dry Sierra Nevada western slope *Ponderosa* pine) occupies a similar altitudinal range, which at these higher latitudes includes upper montane and even borderline subalpine forests (HALLER J.R., 1984). *Pinus ponderosa* sensu lato can there still be met with at 2700 m (SMITH R.H., 1981). A Holocene upper displacement of the altitudinal range approximating such a magnitude is quite unlikely, if *Pinus ponderosa* s.l. were a xerophytic immigrant of southern origin.

The proponents of a Holocene immigration from the South will moreover encounter difficulties in attempting to explain the existence as a relict in the California floristic province of *Pinus jeffreyi* considered to be *Ponderosa* pine's closest relative, but occupying even higher altitudes, and experimentally proven to be phylogenetically older than Sierra Nevada western slope *Ponderosa* pine (JOHANSEN D.A., 1953; MIROV N.T., 1938; McNAIR J.B., unpublished data (see American Journal of Botany 24, 1937, 742) cited by PARRATT M.W. (1967, p.93-94): "*P. jeffreyi* is considerably older than *P. ponderosa*").

If both, var. *ponderosa* and var. *scopulorum* , had simultaneously migrated to the North in the Holocene they would have to be expected to be only slightly differentiated genetically; KUNG F.H. & al. (1972) conclude, however, that the variants must have been separated from one another for several million years.

Pointing at the absence of Early Tertiary macrofossils of *Pinus ponderosa* in the Pacific Northwest (CONKLE M.T. & al 1988) is an artifact resulting from the erroneous notion that *Ponderosae* and *Australes* are not related. The opposite, actually, is the case (see next paragraph), and the claimed macrofossils have, actually, been recovered (see above)! And absence in the Southwest during the later Pleistocene is more parsimoniously explained by the probable individualistic response of tree species to pressures (full glacial episodes) forcing them to migrate (HUNTLEY B. & al., 1989; SPAULDING W.G. & al., 1983). *Pinus ponderosa* must be expected to have been at a serious competitive disadvantage during pluvial episodes, especially if the scenario of a general absence of summer-precipitation in the Interior West during the Wisconsin (SPAULDING W.B. & al., 1983, p.287-290; SPAULDING W.G., 1984, P.62) were a fact. *Pinus ponderosa* probably was, accordingly, a generally very rare species at times. The modern, monotypic pine forests are of very recent origin (MIROV N.T., 1967).

A southern origin and Holocene emigration to the North appears, therefore, to be out of the question. Actually, no hint whatsoever exists warranting the view that *Pinus ponderosa* has experienced a Cenozoic history so much dissimilar to that of other montane conifers in western North America.

2) Nature of the relationship between *Australes* and *Ponderosae*

Most former systematists have - for various reasons - classed all the yellow pines of North America into a common group. However, the most accepted classification today (J.W. DUFFIELD, 1952; see also CRITCHFIELD W.B., 1963a) separates the species of the southeastern United States (subsection *Australes*) from all the western species (subsection *Ponderosae*). But, several aspects indicate that J.W. DUFFIELD's tentative reclassification of the yellow pines of North America is illfounded; illfounded, because this important decision with its profound bearing on our understanding of infrageneric relationships and the systematics of the yellow pines is (almost) uniquely based on the failure to hybridize some "western" *Ponderosae*, with several "southern" *Australes*, but disregarding several other important aspects. These failures have been interpreted as absence of relationship between the two subsections. Moreover, as far as *Pinus ponderosa* is concerned, those who have carried out the experiments seem, unfortunately, not to have considered of importance to specify as well the geographic origin of the *Ponderosa* pine parents used (among other species) in these experiments (the pitfalls of present *Pinus ponderosa* taxonomy!), but it appears (e.g. in CRITCHFIELD W.B., 1966, p.38) that these were generally selected among those growing in the vicinity of Placerville, California, at the Institute of Forest Genetics, in the middle Sierra Nevada, where the hybridization experiments were carried out. Therefore, of the several varieties, and a number of "races" already recognized up to the present to be included in the "single" taxon *Pinus ponderosa*, only one "morphotype/ecotype" (Sierra Nevada western slope *Ponderosa* pine), has actually been tried in these experiments.

A more detailed discussion in paragraph No 4 will demonstrate that *Pinus ponderosa* of the Sierra Nevada probably is only the most recent offspring of the *Ponderosae*, a second grade generation of evolutionary offspring (or secondary vicariad). Very likely, this particular morphotype/ ecotype was, therefore, the least qualified genotype of *Pinus ponderosa* sensu lato to be used in these experiments, since secondary vicariads must be expected to have evolved to an extent which may have already induced genetic incompatibility. Other, more recent hybridization experiments between several geographic "races" of *Ponderosa* pine (CRITCHFIELD W.B., 1984, p.163) have revealed that the Sierra Nevada "race" is only distantly related to the (as will be seen in a subsequent paragraph) phylogenetically much older "race" of the "Pacific Northwest" or "North Plateau". Experiments to hybridize some Southern pines with the phylogenetically older "North-Plateau-races" of *Ponderosa* pine ought also to be carried out. The past and fruitless experiments to hybridize only one "race" of western yellow pine with the Southern pines may, therefore, prove to have deluded former workers into wrong conclusions. Anyhow, it is quite astonishing to note that, in spite of the scantiness of the data finally evaluated to arrive at such a systematically, and conceptually important decision, J.W. Duffields probably erroneous hypothesis, the dissociation of *Australes* and *Ponderosae* into separate systematic groups has never again been questioned, or reconsidered. All to the contrary, this probable misconception has now become so deeply rooted in the minds and opinions of all concerned taxonomists, systematists and other researchers in the yellow pines, that obvious contradictory evidence is deliberately ignored. All recent workers investigating infrasectional relationships of the *Ponderosae*, deliberately leave out *Australes* from their studies, thus virtually indoctrinating and perpetuating the probably erroneous concept of polyphylesis in North American yellow pines. The most obvious evidence objecting to a separation into these unnatural, purely geographical groups, is the similarity of vegetative, and of cone morphology, but also the practically identical cone anatomy (see paragraph 1), similarities so much common to all yellow pines of North America. The evidence derived from these topics strongly advocates a concept of common origin for all these yellow pines. Other causes must be responsible for the failure of hybridization experiments carried out among some of their component taxa.

All those who venture to compare critically similarities in external morphology so much evident among taxa of yellow pines will soon perceive a peculiar phenomenon: Practically the whole spectrum of diversity in external morphology exhibited by the main taxa of southeastern *Australes* reappears, strikingly, as a similar spectrum of variability in the northwestern *Ponderosae*, again in the Cordilleran Region, and apparently also in the complexes of yellow pines in Mexico. In fact, if one studies morphological variation in experimental plots of "*Pinus ponderosa* " grown from seed purchased in the regular trade as having been collected in seed-zones of the "Pacific Northwest", not only the tremendous array of variability displayed by "*Ponderosa* pine of the North Plateau", in what most recent taxonomists still consider to be one and a single taxon, becomes evident, but also (especially in the cones) that the pattern of variability, the sum of similarities and morphological gaps present in "*Pinus ponderosa* of the Pacific Northwest" is practically paralleled by a similar pattern of diversity in the Southern pines, and again in the yellow pines of the Rocky Mountains, and vice-versa.

The pines of subsection *Australes* are members of the mesophytic-temperate forests (DAUBENMIRE R., 1978), therefore of Arcto-Tertiary origin, and, due to past climatic deterioration, now confined to the Southeast of the present United States. Considering the Tertiary general history of vegetation on the North American continent as digested in an earlier paragraph, and although every taxon has its particular, not repeatable history, it seems nevertheless probable that other members of the genus *Pinus* have also had an Early Tertiary widespread distribution, similar to that of the *Pinus strobus* /*P. monticola* / *P. strobus* var. *chiapensis* - phylad already noted. Developing Middle Cenozoic aridity has undeniably not separated the areas of distribution of two parapatric groups, as apparently visualized for *Ponderosae* and *Australes*, virtually along a line of mutual contact which accidentally ran North-South through the now arid Interior West. All to the contrary, the combined consideration of all aspects bearing on the present problem, e.g.

1), the probably widespread Early Tertiary distribution of yellow pine taxa, similar to that already noted in some white pines;
2), the obviously similar northern origin of both, *Australes* and *Ponderosae*;
3), the similar antiquity of these two geographical groups (AXELROD D. I., 1986, p.585);
4), the several common, conspicuous features of external morphology (shapes of female cones, features of cone-scale-apophysis and mucro,

imperfect abscission of mature cones, etc. ...); and especially

5), the practically indistinguishable cone anatomy of recent *Australes* and recent *Ponderosae* which virtually prevents paleobotanists from correctly assigning Eocene and Oligocene permineralized cones and other macrofossils recovered in the Northwest, in the East, and in the Southeast of the continent to either one or the other geographical "group" (see references cited in paragraph 1).

The combined consideration of all these factors strongly warrants the view that the two subsections are quite more closely related to one another than accepted at present, and must, in fact, be visualized as one single, large group.

Clues to corroborate such a statement can also be derived from data hidden in the botanical history of *Pinus ponderosa*. This history (oversimplified for the purpose of these sentences) reveals that several taxa of yellow pines have been described in the past, incidentally from the "Northwest", only to be reduced to synonyms of *Pinus ponderosa* soon afterwards; reduced to synonyms not as a result of comprehensive taxonomic studies, but (almost) solely because seedlings and young plants of all these "morphotypes", grown in Europe from seed collected by explorers (later than David Douglas) in the "Northwest", were so similar in appearance to *Ponderosa* pine .... These "morphotypes" have never been reconsidered by taxonomists; but it is striking to note, for example, that what has been described in the past as *Pinus benthamiana* HARTWEG, is noticeably similar in several respects to *P. engelmannii* in the Cordilleran Region, and to *P. palustris* in the southeastern United States. It may, perhaps, be convenient to add here that conspicuous similarities in several respects between *Pinus engelmannii* and *P. palustris* have already been noted in the past: "seedling growth" (grass stage!, a genetically fixed character) and "the general appearance of the two trees" (long foliage!) are "strikingly similar" (G.B. SUDWORTH, 1917, p.33, 34); "So remarkably do its" (Apache pine) "long needles" ... "resemble the southern longleaf pine that many Southeners mistake it for their well known pine" (ELMORE F.H., 1976, p.113). Modern classifications, however, assign these two species to different infrageneric groupings, to subsections presumed to be unrelated to one another!!.

But, common links to the Mexican yellow pines are also apparent: The "grass stage", this conspicuous feature, is also exhibited by several pines at present included in the Montezuma-complex (MIROV N.T., 1967), and it is only insufficient data on the Mexican complexes of yellow pines which probably prevents us today from perceiving additional, decisive evidence for the existence of common links between West, South-east, and South, of links similar to those of the probable *"benthamiana"/engelmannii/palustris* - lineage. However, *Pinus engelmannii* which apparently has "developed" an amazing genetic distance to "Sierra Nevada western slope *Ponderosa* pine" (PRAGER E.M. & al., 1976; KARALAMANGALA R.R. & al., 1989), can still be easily crossed with (that very same??) "race" of *Pinus ponderosa* (CRITCHFIELD W.B., 1984), perhaps an indication for the cautiousness necessary in evaluating results of hybridization experiments, especially if the resulting data is considered alone, or when the present confusing taxonomy of *Pinus ponderosa* sensu lato is likely to have a profound bearing on the results of studies.

Another example for the probable existence of distinctive lineages is provided by the ecological, and morphological similarities exhibited by what we know as *Pinus washoensis* in the Northwest, and by *P. hartwegii* (*P. montezumae* var. *hartwegii*) in Mexico; or, between one of the "morphotypes" growing at lower altitudes than Washoe pine in the "Pacific Northwest" and *Pinus rudis* (*P. montezumae* var. *rudis*) which replaces *P. hartwegii* at lower altitudes in Mexico.

Obviously, therefore, neither *Australes*, nor *Ponderosae* can be seen as monophyletic groups of own standing; if all the factors elaborated in the present paragraph are considered in common it becomes clear that these unnatural geographical groups, including the *Ponderosae* in Mexico, consist, in fact, of distinct monophyletic lineages the components of which are today more or less equally distributed geographically, among *Australes* in the East, and among *Ponderosae* in the Northwest (*Ponderosa*-complex), and in Mexico (*Montezuma*- and *Pseudostrobus*-complexes), in a similar pattern as exemplified by the *Pinus strobus / P. monticola / P. strobus* var. *chiapensis* - phylad. Moreover, not only *Australes* and *Ponderosae*, also the component groups of the latter, the *Ponderosa*-, *Montezuma*-, and Pseudostrobus-complexes, also appear to be mere artificial groupings: Several of the characters already noted, or discussed in this manuscript and, perhaps, proving in the future to be reliable diagnostic characters in the *Ponderosae*, appear to be evenly distributed among species of several to all of these complexes; e.g. the "grass stage" exhibited by seedlings of *Pinus palustris* and one (!) variety of *P. elliottii* in the East, and by *P. engelmannii* and several forms of *P. montezumae* in the West (MIROV N.T., 1967, p.417); or heptane as a component of oleoresin (see discussion further down); or the feature, upon abscission of the mature cones, of their lowest portion to remain attached to the tree for an indefinite time, a character exhibited by *Pinus palustris* and (either one or both (?) varieties of) *P. elliottii* in the East, and (among others, see also MARTINEZ M., 1948, p.33) by *P. ponderosa*, *P. jeffreyi* , *P. washoensis* , *P. montezumae* , *P. durangensis* , *P. hartwegii*, but obviously not by all *Ponderosae* (e.g. *P. douglasiana*, *P. pseudostrobus* var. *tenuifolia* , etc. ...), nor all *Australes* (information on the presence of this character in particular species had to be gathered from a multitude of sources and may not be complete, neither for the *Australes*, nor the *Ponderosae* in Mexico. However, a similar phenomenon appears to be exhibited by species which are not considered at present to be related to the yellow pines (e.g. *Pinus resinosa* , *P. nelsonii*, etc. ...), but the similarity of the mode of abscission in these cases remains to be investigated). Several other such common characters overlooked, or at present not considered of taxonomic value, or not correctly interpreted (see paragraph No 5), are likely to coexist in (some) *Australes*, and (some) *Ponderosae* , but neither of these characters, no matter if noted, or now and then discussed theoretically, seems ever to habe been studied empirically, or to have been subjected to taxonomic considerations in the yellow pines. Several more or less recently described taxa of Mexican *Ponderosae* typically appear to be well differentiated genotypically (biologically), but intermediate between complexes as to their phenotypic morphological characters (e.g. *Pinus oaxacana*, or the taxon "*apulcensis*", see STEAD J.W. & al., 1984). The taxa now distributed among the three complexes, and *Australes*, will probably have to be regrouped, regrouped into lineages, or phylads, as proposed in this paragraph (a perhaps similar idea has tentatively been proposed already by STEAD J.W. & al., 1984, p.271). The common group *Australes*/ Ponderosae is, primarily, not composed of a number of complexes and taxa, but of a number of lineages, of phylads which in turn are composed of taxa probably having evolved repeatedly in time and which are now more or less equally distributed spatially (see further down and next paragraph); of repeatedly vicariating taxa progressively separated into a sort of three-dimensional pattern of diversity imposed by Tertiary climatic constraints progressively effective spatially and by evolutive processes almost imperceptibly effective (almost imperceptible in conifers in general and the yellow pines in particular) in long periods of (Cenozoic) time. It appears that only such a concept is likely to be consistent with all the available data. As long as these circumstances are not properly understood, and considered - in spite of the difficulties inherent to the task -, true relationships among the multitude of yellow pine genotypes will perhaps be perceived now and then, but in general, taxonomists will continue to be harassed ad infinitum by inconsistencies in the available data, and will continue to clutter the literature, and indexes, with new, only ephemeral names, and/or new combinations, thus more and more adding to the taxonomic and nomenclatoral chaos already existing in the *Ponderosae*. Controversial results obtained by KARALAMANGALA R.R. & al. (1989) from studies in (among others) two geographically distant populations each, of taxa such as *P. michoacana* and *P. montezumae*, and the publication of a multitude of new names and combinations by SILBA J. (1990), may represent good examples to illustrate developments which may be avoided by testing and adopting the profoundly alternative views presented here.

Another factor with an additional bearing on this alternative concept will be discussed more in detail in the ensuing paragraph but ought to be noted here: It is the indication that the allo-, and/or para-, and/or sympatric component taxa of the lineages, or phylads, composing the large *Australes* / *Ponderosae*-group are not always of comparable evolutionary age, but that these component taxa in several cases represent different, consecutive evolutionary generations, or primary and secondary vicariads of one and the same ancestral genome, ecologically differentiated vicariads exhibiting only comparatively slightly evolved (differentiated) characters of external morphology.

Apparently, therefore, it is not absence of relationship between *Australes* and *Ponderosae* which has caused the failure of past experiments to hybridize members of either group. One possible, plausible explanation for this phenomenon may be that "Sierra Nevada western slope *Ponderosa* pine", and perhaps all the so called "*Australes*" (although at least one Southern pine and Sierra Nevada *Ponderosa* pine are likely to appertain to a common lineage), were not only separated spatially, but may also be the product of paleohistoric, and perhapts repeated vicariation in time (Cenozoic), and, therefore, be of a grade of relationship too far off already to still be crossable with one another (see paragraphs 4 and 6). "Morphotypes" of *Pinus ponderosa* of the older "generations" of genotypes, and well selected as to the lineages of yellow pines to which they appertain, those older "generations" surviving to the present in the "Pacific Northwest", must also be tested as to their compatibility, their potential to cross with other members of their own lineage (phylad), but perhaps of different, relative phylogenetic age, and already separated spatially for long periods of time, before results of hybridization experiments can at all be employed to systematize the yellow pines. It is again the pitfalls of the present, confusing *Pinus ponderosa*-taxonomy which are at the origin of the aforementioned probable misconceptions. It is truly necessary to virtually repeat time and again that "*Pinus ponderosa*" of the "Pacific Northwest" has not yet been carefully surveyed botanically. The key for an adequate understanding of diversity in the yellow pines of North America as a whole will never be perceived by studying diversity in the Mexican yellow pines or *Australes* alone; very probably, this key is still hidden, explicitely in the still poorly surveyed diversity exhibited by *Pinus ponderosa* sensu lato, those probably oldest evolutionary "generations" and most complete array of Early Cenozoic yellow pine-genotypes still persisting in the Northwest of the United States!

The conceptual recognition of another probable, and quite different (only western) phylad appears to be equally important to achieve a clear classification of the yellow pines of North America. *Pinus sabiniana* is likely to be of an antiquity comparable to that of the *Ponderosae* (for an evaluation of such a possibility see AXELROD D.I., 1986, p.590; CRITCHFIELD W.B., 1966, p.43). Considering the chemical composition of their gum turpentine (presence of paraffin hydrocarbons), it appears that *Pinus sabiniana* (or its immediate ancestor) has had its share in the origin of *Pinus jeffreyi* (CRITCHFIELD W.B., 1966). Most characters of external morphology in *Pinus jeffreyi* point, however, to a (still extant?) *Ponderosae* as the putative second parent and have, therefore, induced most former workers to join Jeffrey pine systematically to the *Ponderosa*-complex (CRITCHFIELD W.B., 1966). Experiments, again carried out at the "Institute of Forest Genetics" at Placerville, middle Sierra Nevada, California, to hybridize (the phylogenetically older?) *Pinus sabiniana* with (the more recently evolved (once again!) Sierra Nevada-form of) *Pinus ponderosa* have, however, also failed, a circumstance which I to be expected if the presumable phylogeny of the Sierra Nevada-form, as discussed above and in paragraph 4 is proven to be correct. Older "generations" of "morphotypes" of *Pinus ponderosa* sensu lato probably still existing on the "North Plateau" still await to be tested.

Pinus coulteri for the same reason also appears to be a descendant of *Pinus sabiniana* (or its immediate ancestor). Literature does not reveal any suspicions as to the putative second parent; unless one considers a casual statement by N.T. MIROV (1961, p.90) to be more than a clue: He has noticed similarities in chemical composition of the turpentines of *Pinus coulteri* and the "morphotype" of *Pinus ponderosa* occuring on the California Coast Ranges. Other workers have, moreover, reported that *Pinus sabiniana* , *Pinus coulteri*, and the Coast Range-Ponderosa pine (likely to be another true paleorelict) do occur sympatrically at several sites (CRITCHFIELD W.B., 1966, p.37). It would be extremely important to explore whether (natural) hybridization between either of these pines actually occurs in the area, or are at all technically feasible experimentally (*sabiniana*-*coulteri* have been carried out). The pitfalls of present *Pinus ponderosa*-taxonomy appear well to be again exemplified here.

Specific topographic conditions in western North America have enabled many phylogenetically old taxa of plants, obviously with some Early Tertiary yellow pine genotypes among them, to survive the tremendous past climatic changes to the present in refugia in the "Pacific Northwest" and in northwestern California. This region appears, therefore, to be an important key for a proper understanding of diversity in yellow pines as a whole, especially since these pines appear to have originated in this general area, subsequently migrating from there to the East and South. These older northwestern "generations" of yellow pines are likely to have been sympatrically associated to related taxa, at times, from which they are now well separated; and, moreover, they are likely to have evolved but little since at least Middle Tertiary time and may, therefore, still be crossable to one another to an extent (as exemplified by the comparable, and successful experiments to hybridize the older evolutionary "generations" of genotypes in the *Pinus longaeva*/*P. balfouriana*-phylad discussed in paragraph 6), to an extent that would warrant the attempt to reconstruct presumable past hybridization events. It is at least conceivable that *Pinus sabiniana* and the *Ponderosae* had a common ancestor (see MIROV N.T., 1961, p.7) and it may still be possible to verify this hypothesis to some extent in our days.

More recently paraffin hydrocarbons have also been detected in the gum turpentine of several Mexican yellow pines (MIROV N.T., 1967, p.559, also reported by CRITCHFIELD W.B., 1966, p.43), a discovery which led this latter author to doubt the taxonomic value ascribed to this feature by the former worker. Contrary to this, I explicitely sustain its value as a taxonomic character (conspicuously also present in "morphotypes" of both other complexes of *Ponderosae*: In one of the "forms" of *Pinus montezumae* and in *P. oaxacana*, a member of the *Pseudostrobus*-complex) and propose the hypothesis of the existence of a particular (only western), now disrupted phylogenetically old north-south lineage (phylad) of yellow pines differing principally from other yellow-pine phylads by the presence of certain paraffin-hydrocarbons in their gum-turpentine, but a lineage which has otherwise experienced a subsequent Tertiary history exactly similar to that of the other yellow pine-phylads.

D.I. AXELROD (1986, p.624-625) suggests, contrary to this, the *Sabinianae* to be a derivative of an ancestral *Oaxacana*-like group that has been displaced northward with the San Andreas fault system. Such a view, regardless whether proving to be correct in the end or not, strengthens the hypothesis that this morphologically, and biochemically coherent group, the component taxa of which are assigned at present to different systematic entities (*Ponderosae* and *Sabinianae*) ought to be seen as an independent, particular phylad among the other North American yellow-pine-phylads. And in fact, the hypothesis of a South to North displacement appears to be true concerning *Pinus torreyana*, its very narrowly restricted populations on- and on islands offshore of California, and its probable ecological adaptation to originally more southern habitats (a five-needled pine, for an interpretation of the possible ecological significance of needle number in yellow pines see HALLER J.R., 1986 and references cited therein). However, with respect to *Pinus sabiniana* and *P. coulteri*, D.I. AXELROD's hypothesis appears to be inconsistent with all facts relating to *Pinus jeffreyi*: Biochemically this Californian relict is closely related to the *Sabinianae* (MIROV N.T., 1961), but morphologically it is rightly considered to be more related to *Pinus ponderosa* of obviously northern origin; and also the ecological adaptation to could montane environments strongly suggests a northern origin for *Pi-*

nus jeffreyi and evidently also for both of its putative parents.

Contrary to *Pinus jeffreyi* the northern element is perhaps less conspicuously represented in *P. coulteri*: But, this pine is also biochemically related to *Pinus sabiniana*, and also to a *Pinus ponderosa*-"morphotype" of obvious northern origin and documents, moreover, its close relationship to the cold montane *P. jeffreyi* by crossing freely with it wheréever these two pines occur in sympatry. All these aspects rather point to an early evolution of heptane pines (CRITCHFIELD W.B., 1966, p.43, also considers them to be old species) in the North, and to an early migration from North to South and a consecutive Tertiary history quite similar to that of other yellow pine-phylads: Divergent evolutionary component *"generations" of this phylad are today represented by* "morphotypes" and/or taxa in northwestern, and Mexican refugia and the possible paleohistoric South to North displacement of *Pinus torreyana* is only the result of a local facet of the Tertiary geological history of North America.

Incontestably, results of hybridization-experiments carried out among members of the *Sabinianae* and with *Pinus jeffreyi* (CRITCHFIELD W.B., 1966) not always appear at first sight to be in agreement with the hypotheses proposed here. But it has to be kept in mind that experimental hybridization of several combinations of taxa, and several reciprocal crosses have *not yet* been attempted: Of the three artificial crosses having so far been successful among *Sabinianae*, and including *Pinus jeffreyi* , the combination *Pinus sabiniana* (♀) - *P. torreyana* has yielded better results than that between *P. sabiniana* (♀) - *P. coulteri*; however, by far the best results were obtained in crosses between *Pinus jeffreyi* (♀) and *P. coulteri* (CRITCHFIELD W.B., 1966). And obvious inconsistencies may, at least in part, be due to Later Tertiary divergent evolutionary development in *Pinus sabiniana* and *P. coulteri* similar to that of other yellow pine-phylads (vicariation), resulting in decreased crossability among the several genomes of the *Sabinianae*, and with those of the *Ponderosa*-complex (see also paragraphs 3, 4, and 6). But, several aspects bearing on the hypotheses discussed here are still far from being thoroughly explored.

3) Coexistence of divergent evolutionary "generations" of yellow pine genotypes (vicariads)

Middle Tertiary incipient aridity in the interior of the continent of North America has progressively split the wide and continuous Early Cenozoic areas of distribution of yellow pines into finally relictual territories in a pattern as exemplified by the present geographical distribution of the *Pinus strobus / P. monticola / P. strobus* var. *chiapensis* - phylad already mentioned several times: East, Mexico, and Northwest (due to particular topographical and weather conditions the area of retreat extends farther inland in the Northwest and includes areas on both sides of the continental divide in the Northern Rocky Mountains, e.g. in Idaho, Montana, and British Columbia). In yellow pines this recent relictual pattern of distribution is not always as evident as it is in the white pine phylad mentioned above. This is in part due to greater diversity in yellow pines, and in part to the probability that relictual geographical segments of these Early Tertiary genotypes may meantime have become extinct. Presumable yellow pine-phylads have been mentioned in the preceding paragraph: The *Pinus washoensis/P. hartwegii* - phylad (Northwest and Mexico), and the *Pinus "benthamiana "/P. engelmannii / P. palustris* -phylad (Northwest-Cordillera-Southeast; Mexican representatives must still be explored). As proposed in the preceding paragraph the large group *Australes/Ponderosae* probably consists of a multitude of similar phylads, the components of which are more or less similarly distributed geographically today. However, this concept does not yet explain the occurrence of a diversity of yellow pine taxa all through the Cordilleran axis from Montana in the North and far into Mexico in the South.

Two to three additional paleohistoric aspects have probably also had a bearing on the Middle and Later Tertiary evolutionary development of these yellow pine phylads. Among them

1) the presence all through the Tertiary of highlands in the area of the present Rocky Mountains;
2) the Middle Tertiary regression of epicontinental seaways on the continent of North America and the resulting incipient pronounced continentality, and moreover incipient temperature related seasonality of climate (as opposed to an earlier pattern uniquely consisting of dry and wet seasons); the Oligocene crisis; and
3) a diffuse Later Tertiary migratory trend from North to South (apart from Pleistocene oscillations) of yellow pine taxa in the Cordilleran Region.

These paleohistoric aspects and their effect on the proliferation of diversity in (western) *Ponderosae* appear to complicate today the clear perception of the correct pattern of this diversity (the yellow pine phylads and their component taxa).

If the Later Tertiary development of climate in the Interior of the North American continent is adequately interpreted it becomes evident that the (western) *Ponderosae* (already split from their eastern populations (of "*Australes*") further retreated to the West (AXELROD D.I. & RAVEN P.H., 1985, p.40), probably leaving remnant populations in Middle Tertiary uplands in the area of the present Rocky Mountains. For the sake of clarity only "*Ponderosae*" are considered in this paragraph, although the present discussion intends to make clear that some of the aspects named above probably had a somehow similar effect on "*Australes*", and on Mexican yellow pines.

Since Middle Tertiary time these interior upland populations have evolved only very slightly in characters of external morphology, into the "morphotypes" which occupy large tracts of the Cordilleran axis on the territory of the United States today, e.g. *Pinus ponderosa* "var. *scopulorum*", and *P. engelmannii*. Several former taxonomists have pointed out the difficulties encountered in separating these morphotypes from their obvious ancestors of (parts of) the Pacific Slope by using botanical characters alone (SHAW G.R., 1914; SUDWORTH G.B., 1917). And, in fact, if compared to the morphotypes persisting in the Pacific Northwest, these interior vicariads appear to exhibit a very similar pattern of variability, as exemplified by the probable *Pinus* "*benthamiana*"/*P. engelmannii*/*P. palustris*-phylad. The existence of similar parallelisms in external morphological characters between other northwestern (e.g. *Pinus washoensis*) and Rocky Mountain "morphotypes" (several of these appear at present to be included in the taxon *Pinus ponderosa* var. *scopulorum*) is not only perceptible to anyone studying fresh or dried material from these areas, but can also be extrapolated from observations unconsciously and casually reported by several recent workers (AXELROD D.I., 1986, p.589; CRITCHFIELD W.B., 1984, p.164; but see also MIROV N.T. & al., 1976, p.77). One conspicuous, although ephemeral character distinguishing between all the northwestern components on the one hand, and all the Cordilleran components of yellow pine phylads on the other hand, is immature female cone colour which appears to be dark purple in all northwestern, and is green in all Cordilleran "morphotypes" (see discussion of this character in paragraph 6).

From the preceding discussion it becomes clear that the northwestern (Pacific Northwest, or North Plateau) relict components of these yellow pine phylads must be phylogenetically older than their Rocky Mountain vicariads. And, in fact, paleobotanists consider the Rocky Mountain flora to have a more modern aspect as compared to that of the Northwest, and Rocky Mountain taxa of pine to generally correspond in external morphological characters to taxa of the Oligocene (AXELROD D.I. & RAVEN P.H., 1985, p.30, 38), while modern taxa of pine of the Pacific Slope (which continued to retreat until a later period of geological time) generally correspond to the morphotypes that lived in the area in Miocene time (AXELROD D.I., 1976, p.14, 24).

It seems sound, therefore, to consider the Rocky Mountain "morphotypes" of yellow pines to be of practically Oligocene age, especially if the fact of a pronounced contemporaneous climatic deterioration is taken into account: Some paleobotanists have termed this deterioration "terminal Eocene event" (WOLFE J.A., 1978), or at least "Oligocene crisis" (AXELROD D.I., 1987, p.65). Genomes of the extremely conservative genus *Pinus* require virtually strong constraints to evolve and to express evolutionary change in development of distinguishing characters of external morphology. As a consequence of this particularity the modern morphotypes of Rocky Mountain yellow pine vicariads are hardly distinguishable, or at least difficult to separate from their northwestern ancestors, which appear to have changed even less; Pacific Slope and Cordilleran "morphotypes" can be difficult to separate at times, unless immature female cone colour is also considered. And the postulate that Mid-Tertiary evolutionary change in Rocky Mountain *Ponderosa* pine was practically restricted to change in immature cone colour is further corroborated by an obviously similar development in several other taxa of *Pinus*, and even other *Pinaceae* (!!) of the western United States (and elsewhere in the northern hemisphere !!); this relatively minor evolutionary change, only in immature female cone colour, appears to be the result of forcing originating from incipient temperature related seasonality, and concomitant incipient continentality of climate (see paragraph 6).

Each of the components of yellow pine phylads, those in the Northwest and those on the Cordilleran axis still require their particular minimum amount of summer precipitation for persistence. Absence of summer rain did finally gradually eliminate the phylogenetically older components of yellow pine phylads from the increasingly arid Intermountain Region and did restrict their distribution in Miocene to Pliocene time to the Northwest with its even today generally more equable climate: absence of summer rain at the same time prevented the genealogically younger Rocky Mountain vicariads to invade the same territory, although they would appear to already have become adapted to incipient continentality and temperature related seasonality of climate, to the other elements of climatic change in the area. Such a view seems to be more consistent with paleohistorical facts than the hypothesis of the extinction of *Pinus ponderosa* in large tracts of the Intermountain Region during an interglacial hypsithermal (as suggested by AXELROD D.I., 1976, p.22, 53; AXELROD D.I., 1986, p.586). The vicariads appear to have been separated from their ancestors for a much longer interval of time (AXELROD D.I., 1986, p.589; CRITCHFIELD W.B., 1984, p.164, 167; CRITCHFIELD W.B. & ALLENBAUGH G.L., 1969, p.24; KUNG F.H. & WRIGHT J.W., 1972, p.84). It is only the present confusing taxonomy of the *Ponderosa*-complex which seems to have prevented these workers from reaching similar conclusions.

The comparatively minor diversification of the Rocky Mountain vicariads since obviously Oligocene time (more than 30 Ma ago) from ancestors which, on the contrary, appear to have remained practically unchanged and are still persisting today on the "North Plateau" stresses the belief that Pleistocene and Holocene (1 to 2 Ma) were intervals of time (times of rapidly oscillating climate!) not long enough to induce macroevolutionary change in a conservative conifer taxon, e.g. *Pinus ponderosa* sensu lato, neither on the Cordilleran axis, nor in the relictual "morphotypes" of the Northwest. Presumed perception of variability in *Pinus ponderosa* sensu lato in this area may only be a misinterpretation of a diversity yet poorly understood, and this diversity is probably only classifiable with a taxonomic concept more consistent with the probable historical biogeography of the whole complex.

It seems clear that ancestral yellow pine-morphotypes in the East ("*Australes*"), and in Mexico have probably experienced a similar history, although only younger vicariads appear to persist in the Southeastern United States today; contrary to areas in Mexico, purple coned morphotypes, the presumable ancestors of the green coned presumably Oligocene vicariads, have so far not been reported to exist among the so called "*Australes*". Data on immature cone colour in *Pinus* is poorly documented in the literature but several purple coned yellow-pine morphotypes are known to exist in Mexico (e.g. *Pinus hartwegii*, *P. rudis*, etc. ...). But, a far greater diversity of yellow pine ancestors than that persisting to our days must have been at the origin of the huge diversity of green coned vicariads colonizing the Mexican Highlands today; and these vicariads appear to have evolved more to the North, on the Cordilleran Axis. Late Tertiary climatic deterioration finally forced several persisting ancestors together with the phylogenetically younger vicariads to migrate to the South (secondary migration), to the area they occupy at present, into areas then recently deserted by the Neotropical-Tertiary element of the North American flora. This view is corroborated by macrofossils similar to *Pinus engelmannii*, *P. michoacana*, and *P. montezumae* found in late Oligocene strata of Colorado, and macrofossils similar to *Pinus pseudostrobus* found in Miocene strata in Nevada (AXELROD D.I., 1986, p. 586). Many of the species of yellow pine in Mexico, whether phylogenetically older, or younger components of their respective phylads, have, therefore, retreated to the South in the Neogene, to a climate they still can cope with. All these yellow pine-phylads, and their component taxa occupy at present more or less allopatric, parapatric, and in some cases perhaps even sympatric areas, and in such a way contribute to the generally erroneous assumption that the highlands of Mexico are today a secondary center of evolution in *Pinus*, although, on the other hand, presently active evolutionary processes in particular species cannot definitely be ruled out with our present, limited knowledge. For example, too limited knowledge probably yet impedes a satisfactory explanation for the origin of *Pinus ponderosa* var. *arizonica*. Some authors (e.g. LOOCK E.E.M., 1950: MARTINEZ M., 1948) have discerned similarities between var. *arizonica* and *Pinus durangensis*. Var. *arizonica* as a five-needled pine may, perhaps, be more related to *Pinus durangensis* (and its phylad?) than to *P. ponderosa*, and of Later Tertiary origin, at times when *P. durangensis* may have been compelled to retreat to the South.

The ancestral "morphotypes" of *Pinus ponderosa* sensu lato still persisting in the Northwest are considered here to represent a conglomerate of the phylogenetically oldest still existing component "generations" of their respective phylads. Contrary to this, the yellow pines now included in "*Australes*" represent a conglomerate of phylogenetically younger component "generations" of probably these very same phylads. Therefore, divergent evolutionary development of taxa of "*Australes*" is obviously more advanced than that of "morphotypes" of *Pinus ponderosa* sensu lato of the Northwest. Such a state of affairs may convincingly explain why taxonomic diversity seems to be undisputed in "*Australes*", while the aggregation of "morphotypes" in *Pinus ponderosa* sensu lato in the Northwest is still misinterpreted as an array of tremendous variability exhibited by only one single genotype. However, these northwestern "morphotypes" virtually are at the origin of a multitude of distinct and independent yellow pine-phylads, *the components of which are the more differentiated today* (e.g. "*Australes*") the more they are the result of repeated vicariation (this very same effect only is virtually counterbalanced in the Southwest by the far greater diversity exhibited by Mexican *Ponderosae*).

The concept of a dual line of antiquity in (Mexican) *Ponderosae* may fragmentarily have been noticed already, earlier by another worker (HALLER J.R., 1975). All the phylogenetically younger vicariads along the Cordilleran axis still constitute an Arcto-Tertiary element (AXELROD D.I. & RAVEN P.H., 1985, p.38).

4) Origin of the Sierra Nevada western slope *Ponderosa* pine

Pinus strobus and other conifers (e.g. *Abies balsamea-A. fraseri / A. lasiocarpa-A. lasiocarpa* var. *arizonica* ; *Pinus banksiana / P. contorta*; etc. ...) are examples for the present conspicuously disjunct or relictual distribution of probably more widespread Early Tertiary phylads. Another conspicuous instance for a quite different stepping-stone like pattern of migration and distribution from North to South, as proposed for the phylogenetically younger *Ponderosae* in the Rocky Mountains, is exemplified by the "natural line" *Pinus flexilis - P. strobiformis - Pinus ayacahuite* (AXELROD D.I., 1986, p.579, and 601; MIROV N.T., 1967, p.327, 387, and 546). *However, the reason for citing this example under the heading of* this particular paragraph is to exemplify a still different pattern of migration. *Pinus flexilis* is, moreover, known to have as well migrated, among several other taxa of plants of the Rocky Mountain floristic province, across the southern "Great Basin" into the southern Sierra Nevada and the southern California Transverse Ranges (AXELROD D.I. & al., 1985, p.41; AXELROD D.I., 1986, p.590). An account of the probable time and mode of this migration, set down in a different context (AXELROD D.I., 1959), is written so vividly, that a comprimated repetition in the present context is likely to be rather imperfect; to avoid confusion readers are specifically referred to this account.

In short terms, an ancestral Nevadan Late Miocene forest, including Rocky Mountain elements, migrated to the windward slopes of the Sierra Nevada (*Pinus ponderosa* specifically enumerated) as the mountain range began to be lifted (AXELROD D.I., 1957), and as, consequently, rainfall (especially summer rain) decreased to the East during Pliocene, thus acting on the varying ranges of tolerance of the species composing the forest, some of which modified into ecotypes better adapted to the new environments (AXELROD D.I., 1959).

However, two very important implications strongly indicated by such a history have not yet been considered (see AXELROD D.I., 1976; AXELROD D.I., 1977; AXELROD D.I. & al., 1985; AXELROD D.I., 1986; etc. ..., nor does any other author seem to have taken up this particular subject): Firstly, the Sierra Nevada western slope *Ponderosa* pine, this, in fact, "archetype" of *Pinus ponderosa*, to which several other taxa have been classed as varieties, simply must be envisioned as a Pliocene offspring, or secondary vicariad of (one of) the Middle Tertiary interior (Rocky Mountain) primary vicariads of *Pinus ponderosa* sensu lato (and not vice-versa), which in turn are probable descendants of still older "generations" of *Ponderosae* (see further down for discussion of putative closer relationship to older lineages). Again, "typical" *Pinus ponderosa* (Sierra Nevada western slope) appears to have evolved more in its ecological adaptations (AXELROD D.I., 1976, p.51), rather than in more conspicuous features of external morphology of reproductive organs so important to the classification of the genus *Pinus*. In this instance it must be remembered that eminent former taxonomists (among them G.R. SHAW, 1914; G.B. SUDWORTH, 1917, p.29, but also some recent researchers rather prefer to adher to such a view) have denied the presence of constant morphological dissimilarities between "typical" *Ponderosa* pine and variety scopulorum (or whatever was, and is considered to be included in it). Mio-Pliocene volcanism in the Sierra Nevada was followed by diastrophism all through the Pliocene and Early Pleistocene (AXELROD D.I., 1957). Some 2 to 10 Ma of wide ecological opportunities to colonize new ground, and severe climatic constraints (Pleistocene climatic deterioration and fluctuations, evolving Mediterranean climate) apparently were factors not strong enough to induce distinctive macroevolutionary changes in the conservative conifer taxon *Pinus ponderosa*, a fact which once again casts doubt on the postulate of present time evolutive processes, discernible to the taxonomist, being active in *Pinus ponderosa* sensu lato in the Pacific Northwest. Considering its probable complex history, poor crossability of Sierra Nevada western slope *Ponderosa* pine with "races" of *Pinus ponderosa* sensu lato of distant ancestry in the Pacific Northwest is to be expected.

The conclusion that "typical" *Pinus ponderosa* (Sierra Nevada western slope) is of rather recent origin, is further substantiated by results of three independent investigations overlooked to the present (mode of archegoniogenesis, JOHANSEN D.A., 1953; degree of saturation of seed oils, MIROV N.T., 1938; phylogenetic interpretation of glyceride properties, unpublished data by McNAIR J.B., 1937, cited by PARRATT M.W., 1967, p.93-94), which consider *Pinus jeffreyi* (morphologically a *Ponderosae*, but biochemically a *Sabinianae*) to be phylogenetically older than "typical" Ponderosa pine of the Sierra Nevada. Hybridization experiments (CRITCHFIELD W.B., 1984) have, moreover, shown the western slope Sierra Nevada Ponderosa pine to be less related to *Pinus ponderosa* of the "North Plateau" than to one geographically remote form of the "taxon" scopulorum. These, and several other circumstances cited in this manuscript do splendidly fit into the theses presented here. I have several times emphatically attempted to explain in this paper that "typical" western slope Sierra Nevada Ponderosa pine lacks proper qualification to be used as only western parent in hybridization experiments with members of subsection *Australes*, or with *Sabinianae*. These statements hopefully will now be better understood, since the probable paleobotanical history of the aggregate *Pinus ponderosa*, as outlined above, implies that the genotype of the Sierra Nevada western slope probably is genetically too distant already to be yet fully crossable with all other evolutionary components of its own phylad, let alone to component "morphotypes" of other phylads composing the large group *Australes / Ponderosae*. Individuals of *Pinus ponderosa*-"morphotypes" from the "Pacific Northwest", of the phylogenetically older "generations" of these morphotypes still await to be tested experimentally as to their hybridization-behaviour with *Australes* and *Sabinianae*.

It is interesting to note in the present context that D.I. AXELROD (1986, p.579), MARTINEZ M. (1948), and others, have found similarities in cone morphology between *Pinus lambertiana*, a common associate of Sierra

Nevada Ponderosa Pine, and *Pinus ayacahuite* of Mexico. Since the "natural line" *Pinus flexilis*, *P. strobiformis*, and *P. ayacahuite* can be expected to have experienced a Cenozoic general history comparable to that also probable for *Australes/Ponderosae*, a search for ancestors to *Pinus lambertiana* among relicts of this natural line in Mexico (*Pinus ayacahuite*, or a putative ecotype, is likely to have had a more northern distribution earlier in the Neogene) may, perhaps, be more realistic than to uniquely point at the admittedly interesting, surprising, and yet inexplicable crossability of Sugar pine with certain Asian white pines (see detailed elaboration of present knowledge in CRITCHFIELD W.B. & al., 1986). The *Abies concolor*-complex may be another example for a paleohistory similar to that in *Pinus ponderosa* and in the *P. flexilis*-phylad: An old (purple cones) and its primary vicariad lineage (green cones, see paragraph No 6) are parapatrically associated in the Southern Rocky Mountains today but each maintains genetic integrity. *Abies concolor*, var. *lowiana* (green cones), their again only slightly differentiated secondary vicariad is a common member of Sierra Nevada forests. The *Pinus contorta/P. banksiana* phylad, *Abies balsamea* and *A. fraseri/A. lasiocarpa* and *A. lasiocarpa* var. *arizonica* have already been named. Several putative phylads among the genera *Abies*, *Picea*, *Tsuga*, and *Pseudotsuga* ought perhaps also to be reevaluated in the context of the probable Tertiary general history of vegetation on the continent of North America.

Pinus flexilis, former member of an ancient Miocene interior (Rocky Mountain) forest, as has already been stated above, has survived to the present as a relict in the southern Sierra Nevada, and in the California Transverse Ranges. Another implication inherent to such a paleohistory is an expectable similar survival of interior (Rocky Mountain) *Pinus ponderosa*, "variety" *scopulorum*, in these very areas. And, in fact, very scattered data already present in literature permit to tentatively suggest its presence there. At present this "taxon" actually is reported only as far west as the Spring Mountains in southernmost Nevada (CLOKEY I.W., 1951, p.28), but not from California. But, *Pinus ponderosa* in the southern Sierra is of smaller stature than its relatives farther North (DUDLEY W.R., 1896); *Pinus ponderosa* on the eastern slopes of the Sierra Nevada is differing ecologically (and also silvically) from its kin on the western slopes (HALLER J.R., 1961); the eastern slope of the Sierra Nevada is markedly influenced by the "Intermountain flora", expecially in Central California (REVEAL J.L., 1980, p.47-48); putative biochemical and other hybrids between western slope Sierra Nevada Ponderosa pine, and "variety" *scopulorum* have consistently, and primarily, been reported from the eastern edge of the Sierra (MIROV N.T., 1930, p.532); W.B. CRITCHFIELD (1984, p.145-146) summarizes other data consistent with the present hypothesis and considers the populations of *Pinus ponderosa* in southern California Mountains to be a distinct "race"; D.A. JOHANSEN (1953) reports of trees (in far upper end of San Antonio Canyon in the San Gabriel Mountains) at present known to be *Pinus ponderosa*, the archegonial characters of which, however, "are so radically different from those of (*Pinus ponderosa*) that they are either hybrids of constitute an unrecognized species"; etc. ..., etc. ...; western slope Sierra Nevada Ponderosa pine survives with practically no summer rain at all (AXELROD D.I., 1976, p.34); "variety" *scopulorum* (in the Interior) only thrives where there is at least some summer precipitation; so does *Pinus flexilis* in southern California, in places where there is at least a minimum of summer rain (RAVEN P.H. & al., 1978, p.48, 59, 60). It is the overall configuration, and especially the probable paleohistory of Miocene Nevadan forests, as outlined above, which corroborate the belief that genotypes of "variety" *scopulorum* may actually be extant in California, and may have to be looked for. The relatively small morphological differences between the two varieties may account for the fact that Rocky Mountain "variety" may have remained phenotypically hidden among the genotypes of *Pinus ponderosa* sensu lato in the area.

Another tentative suggestion needs similar, thorough testing: As has been stated above, the westernmost outlyer of "variety" *scopulorum* trives in the Spring (Charleston) Mountains in southernmost Nevada, a topographical extension of the Mogollon Rim in Arizona. I also have already alluded to statements of several workers which allow to tentatively extrapolate the existence of more than one distinct genotype within "variety" *scopulorum* (AXELROD D.I., 1986, p.589, comparing *P. washoensis/P. scopulorum*; CRITCHFIELD W.B., 1984, p.164, comparing morphological characters in both, *Pinus washoensis*, and "typical" *Pinus ponderosa* to those in the Rocky Mountain "variety" growing in the eastern Great Basin, and in populations of this "variety" still farther to the Northeast). The probable correctness of such an extrapolation is also corroborated by data inherent to the pattern of diversity discernible in *Pinus ponderosa* sensu lato of the Pacific Northwest, the probable ancestors of the vicariads at present designated as "variety" *scopulorum*. MIROV N.T. & al. (1976, p.77), report, moreover, of additional, biologically quite distinct populations of "variety" *scopulorum* in Arizona, perhaps a very significant discovery. Whether a more northern form of "variety" *scopulorum* (across the "Great Basin"), or the biologically quite distinct population in Arizona (across the Mogollon Rim) has actually contributed to the Rocky Mountain - race probably present in southern California, and to the origin of Sierra Nevada western slope Ponderosa pine, must be determined by experiment. It has to be kept in mind in this context that Sierra Nevada western slope Ponderosa pine, although genetically quite distant already, inexplicably is still fully crossable to *Pinus engelmannii* of southern Arizona and northern Mexico.

5) Putative complementary diagnostic characters in the *Ponderosae*

I believe that the foregoing paragraphs have convincingly demonstrated that a reliable phenetic distinction of the diversity in *Ponderosae* can only be achieved with additional, complementary diagnostic characters. Proposals to a similar effect, especially to also consider "external field characteristics" in conifer-taxonomy, have already been advanced earlier by other workers (e.g. SILBA J., 1989; TOMLINSON P.B. & al., 1989). Other workers already have considered additional characters (e.g. HALLER J.R., 1962), or noted, more or less casually, some even ephemeral characteristics, such as immature male, and female cone colour (AXELROD D.I. 1986, p.589; CRITCHFIELD W.B., 1965; CRITCHFIELD W.B., 1984, p.146, 153, 160, 161; etc. ...).

But, taxonomy of the *Ponderosae*, as a rule, is still primarily based on the same diagnostic characters on which the early classifications of the genus *Pinus* were based. Methods of numerical taxonomy (computing as a rule the very same characters that have not yielded convincing results in conventional taxonomy) have recently been applied to the Mexican yellow pines (STEAD J.W., 1983); hybridization-behaviour (investigations into predominantly limited sections of the problem and with several misconceptions as points of departure have led to sometimes too premature conclusions, camouflaging, rather than manifesting true relationships, especially in the *Ponderosae*; see CONKLE T.M. & CRITCHFIELD W.B., 1988, for a comprehensive review of experiments already carried out), and aspects of turpentine-chemistry have, to some extent, been investigated in the

Ponderosa-complex (MIROV N.T., 1961; 1967; who's results appear to generally conform already now to the theses presented here). However, appropriate sampling for any kind of investigation, whether into hybridization-behaviour or turpentine-chemistry, variability of characters of seeds or any other characteristic, is again largely dependent on a more reliable delimitation of putative genotypes by phenetic taxonomy. In the past, however, samples, if at all specified as to their source, appear to have been collected mainly according to geographical considerations, and completely disregarding other criteria. Especially *Pinus ponderosa* sensu lato in the Pacific Northwest has not yet been adequately surveyed botanically. This circumstance certainly has falsified the results of many a study and may be responsible for many an inconsistency. A large body of incoherent data on leaf-anatomy, and -histology in *Pinus ponderosa*, available throughout the literature, is almost useless, since, as a rule, no indication is provided as to the source of the investigated material (poorly understood diversity has resulted in a very conservative taxonomy and, as a consequence, information on the origin of material is often thought negligible). The crucial importance of the source of material (samples) to the result of investigations in *Pinus ponderosa* sensu lato and to their interpretation is best exemplified by the existence and confusing discussion of several "races" of Ponderosa pine on the Pacific Slope. "Races", contrary to taxa, are excluded from taxonomic and nomenclatoral indices, and from generalized floras; their existence and identity is therefore not readily retrievable to researchers other than true specialists of the particular taxon.

Some remarkable characters present in some *Ponderosae* (or *Australes*) have, now and then, been noted, but apparently never been empirically investigated for their actual distribution among the yellow pines, or their diagnostic value: among them the "grass stage" and the "imperfectly abscised cone", or external characters of seeds.

In the field, however, other such particular, truly diagnostic characters, not yet recorded in literature and sometimes ephemeral, are certain to exist; for the sake of a more dependable taxonomy in the *Ponderosae* they ought to be sought for by close year-round observation in the field (at more or less close intervals depending on the observed character). Ephemeral, but diagnostic characters ought, therefore, to be also preserved for the herbarium as best as possible with regular procedures (some improvements have already been proposed, e.g. PAGE C.N., 1979), but additionally as photographs of diagnostic (macrophotography) quality.

Among the field-characteristics deserving to be given more attention in taxonomic considerations in the *Ponderosae* are characters of the branchlets in their first and second year, characters of the bark, ecological differences, shape of tree-crowns, but most important of all reproductive phenology, and ontogeny (including external characters they exhibit during ontogeny) of male conelets and female flowers/cones from the time of budbursting to maturity. Phenology of flowering appears to be perhaps only sporadically significant in the *Ponderosa*-complex (more or less overlapping optimal time of flowering), but a very important comparative diagnostic character in *Australes* and the Mexican *Ponderosae*. Phenology of cone-ripening, on the other hand, seems to be of diagnostic utility in the *Ponderosae* as a whole (SCHOPMEYER C.S., 1974; and additional data very scattered in literature). Among the characters most important during ontogeny of male and female reproductive structures are size, and colour of staminate cones ultimately before maturity, and colour of developing immature female cones.

Purple immature female cone colour in *Pinus ponderosa* was noted for the first time by C.S. SARGENT while reconnoitring the West for his "Report on the Forest trees of North America" (Catalogue of the Forest Trees, Tenth Census of the United States, Volume 9, 1884, p.192; Silva of North America, volume 11, 1897, p.78) and by G.B. SUDWORTH (Forest Trees of the Pacific Slope, 1908, p.43; also 1917, p.31). Verbal discussions of the subject among specialists (not recorded in the literature) appear to have induced the most eminent of contemporary connoisseurs of pines, G.R. SHAW (1933), to settle once and for all the controversy on the dark immature cone of *Pinus ponderosa*: In order "to prevent further error from that source" he determined "the purple color (to be) a transient intermediate stage between the summer-green and the autumn-brown coloration of the maturing cones" - a foundamental error!. The opposite, in fact, appears to be true: In *Pinus ponderosa* sensu lato of the Pacific Northwest (including *Pinus washoensis* and *P. jeffrey* !) to my knowledge all immature cones of all trees are dark purple for the whole interval of time between bud-bursting (flowers/conelets) until almost to maturity. But I have consistently observed on a multitude of trees planted for ornament and for silvical purposes that the purple pigment more or less vanishes approximately four weeks prior to the time the cones begin to dry at maturity. During this time most cones display various shades from bright grass-green to a very dark blackish green (also in *Pinus washoensis* and *Pinus jeffreyi*). Cones of these species consistently mature (open) in August if the trees are grown side by side at low elevation, while the consistently green cones of Sierra Nevada western slope Ponderosa pine open in mid-September, and those of variety *scopulorum* (always green) from end of September until well into October. The basically green female flowers, sometimes more or less tinged with red, of Sierra Nevada western slope Ponderosa pine, and variety scopulorum, appear, without exception to always turn into green cones retaining this colour until they dry at maturity. The green stage of immature cones of *Pinus jeffreyi*, *P. washoensis*, and *Pinus ponderosa* sensu lato of the Pacific Northwest, an as yet unrecorded characteristic, at low elevations, consistently appears in the middle of July and, consequently, is certain to be displayed accordingly later at higher elevations.

One of the most intriguing inconsistencies in *Pinus ponderosa* sensu lato, variation in immature cone colour (green at low to purple at high elevations) on an elevational gradient from northeastern California into southwestern Oregon (SMITH R.H., 1981), interpreted as introgressive hybridization between Sierra Nevada western slope Ponderosa pine and *Pinus washoensis* (HALLER J.R., 1984; 1987), but not similarly supported by other evidence, may perhaps be more parsimoniously explained by this curious change in immature cone colour in July and August, prior to maturity. R.H. SMITH noted variation in colour according to altitude between 1200 and 2400 meters in "mid-August", 1978. The call to also adequately consider "external field characteristics" (SILBA J., 1989) seems well exemplified, should this, for its simplicity, almost sacrilegious attempt to alternatively interpret earlier observations by other workers prove to be true. The variants in cone colour, or "hybrids", moreover display no similar variation in the composition of their gum turpentine, neither along, nor at the lower or upper edge of the elevational gradient! R.H. SMITH's transect ought to be revisited to see if his observations would not have been different earlier in the summer.

Differences in colour of immature female cones between the older lineages in the Pacific Northwest and the primary and secondary vicariads in the Rocky Mountains and Sierra Nevada western slope are accompanied by similar differences in the colour of the staminate cones ultimately prior to maturity: Those in *Pinus ponderosa* sensu lato of the Pacific Northwest and *Pinus washoensis* are uniformly deep purple (sometimes tinged with violet) including the crest of the anthers. Those in *Pinus jeffreyi*, in variety *scopulorum*, and in Sierra Nevada western slope Ponderosa pine are basically greenish to yellowish (or orange), sometimes more or less tinged with red; or entirely rose to bright red or carmine (but never purple!). However, the round crests of the anthers are always distinctly lighter coloured, or even white(!), a design always ensuring a clear distinction.

6) Significance of immature female cone colour to taxonomy and to phylogenetic reconstruction in the *Ponderosae* (*Pinus* and *Pinaceae* in general)

General Cenozoic history of the vegetation of North America (as outlined by D.I. AXELROD, and others, in a multitude of papers, of which, for the sake of space, only a minority can be cited here, see literature-citations; see also DAUBENMIRE R., 1978) indicates that the "Pacific Northwest" of the United States, and northwestern California, are refugia, especially for conifers, that were much more widespread earlier in the Tertiary, when climate was warmer, but also more equable. It has been stressed in this manuscript that developing, Later Tertiary continentality, and seasonality of climate have exerted similar constraints on Early Tertiary lineages of *Australes / Ponderosae*; that their populations in the Northwest are, in fact, relicts of a once more ubiquitous distribution having retreated into an area of relative equability of climate, as compared to the severe continental climate prevailing in the Interior West. I hope to have convincingly shown that the *Ponderosae* in the Rocky Mountains (probably) are mere vicariads of their probably in several cases extant relict ancestors in the Northwest; and that these vicariads thrive in a severe continental climate inasmuch as their ecological requirements for at least a minimum of summer precipitation are met with. A secondary vicariad appears to have adapted late in the Tertiary to more Mediterranean climate on the western slopes of the Sierra Nevada in California. The aggregate *Pinus ponderosa* sensu lato may, in fact, perhaps be the only "taxon" among the *Ponderosae*, in which the relatively complete sequence of Cenozoic evolutionary development is still extant. The Cenozoic pattern of diversification in the *Ponderosae*, and perhaps in *Pinus* in general, appears to have been "vicariance", and taxa seem to be more easy to delimit the more of these vicariads in between have become extinct;

and conversely, in "taxonomically difficult groups" (e.g. *Ponderosae*, some East Asian complexes of *Pinus*, different groups in other *Pinaceae*) several to most of these vicariads appear to be still extant, thus contributing to their complexity.

Ancestors and vicariads in *Pinus ponderosa* sensu lato differ only comparatively slightly in external morphology. But they exhibit a very striking dimorphism in immature female (and also male) cone colour: Young female cones of all genotypes of *Pinus ponderosa* sensu lato known to me to occur in the Pacific Northwest, including *Pinus washoensis*, exhibit a dark purple to almost black colour during practically the whole time of their ontogeny, as compared to the always and, without exception, uniformly green cones in all primary, and secondary vicariads (see also AXELROD D.I., 1986, p.589; CRITCHFIELD W.B., 1984, p.163-164). Dark immature female cone colour at first thought appears, therefore, to characterize Early Tertiary lineages of *Pinus ponderosa* sensu lato, and cones always remaining green between time of flowering and maturity appear to characterize both, the primary vicariads (probably Oligocene), and secondary vicariads (probably Pliocene, see discussion in preceding paragraphs). Purple coned *Pinus jeffreyi* has, moreover, in three independent studies been considered phylogenetically older than green coned Sierra Nevada western slope Ponderosa pine (JOHANSEN D.A., 1953; MIROV N.T., 1938; Mc NAIR J.B. (1937) cited by PARRATT M.W., 1967).

This idea may appear far-fetched at second thought. However, the more one gathers data on immature male, and female cone colour in conifers, the more one must gain the conviction that the pattern, and geographic distribution, of colour dimorphism cannot be a matter of mere accident, but, to the contrary, must be highly significant. More examples of sister taxa, exhibiting immature cone colour dimorphism are not only also extant among the complexes of *Ponderosae* in Mexico (e.g. *Pinus hartwegii*, *P. rudis* among the *Montezumae*, *P. douglasiana* and others in the *Pseudostrobus*-complex), among other western pines (e.g. *Pinus longaeva* / *P. aristata*), or in the Old World (*Pinus heldreichii* and *P. leucodermis*/ *P. nigra*), but also well represented in the other larger genera of *Pinaceae*, and holarctic in distribution. The following data has mainly been assembled to further corroborate the belief that dark purple immature female cone colour is a conspicuous characteristic of Early Tertiary lineages in the *Ponderosae*, in the genus *Pinus*, and perhaps in *Pinaceae* in general. Immature female cone colour, to my knowledge, has so far only once been considered a feature relevant to phylogenetic reconstruction in conifers. LIU T.-S. (1971) believes (although he does not state the findings on which his opinion is based) that green immature cone colour is primitive in *Abies*. A diametrically opposite view is suggested here, but this tentatively proposed hypothesis admittedly depends largely on the correctness of the paleohistory of the *Ponderosae* as outlined in earlier paragraphs of this manuscript.

In many *Pinaceae* all immature female cones of all trees display, as a rule, a single colour, various shades of green (yellowish-green to dark green); but in some taxa all, or part of the green cones, while developing, are sometimes tinged with, or are turning into shades of red, or even darker colours before becoming brown (in different shades) at maturity. Cone colour dimorphism for a more or less long lapse of time before maturity in basically green coned species is known to occur in *Abies grandis*, *Picea glauca*, *P. abies*, *P. engelmannii* (its immature cones are sometimes reported to be reddish green and green, but sometimes described as being truly purple?), *Pinus monticola* (?, data not very clear), *P. strobiformis*, *P. sylvestris*, *Pseudotsuga menziesii*, etc. ... Their immature female cones still are basically green; these cones, and the trees bearing them, will here be termed green cones, or green trees, and are not of particular interest in the present context, unless they represent green coned sister taxa (populations) to truly purple coned species as commented on below.

A number of species (or populations within taxa) in several genera, however, only bear immature cones uniformly coloured violet, or purple to almost black (very dark as a rule), from the time of bud-bursting to maturity (or almost to maturity, as in some purple coned *Ponderosae*); at maturity (after one season in most genera, or after two seasons in *Pinus*) these dark cones turn into different shades of brown; more often into reddish-brown, sometimes into dull brown, and seldom into yellowish-brown; into shades of brown which are preserved in herbarium specimens according to the rate of maturation of cones or the length of time elapsing between maturity and collection. These dark coloured immature cones, and the trees bearing them, will here be termed violet/purple cones, or violet/purple trees, and it is this pattern that is significant in the context of this paragraph, but emphasis must be placed on uniformly dark (as a rule) colour displayed by all cones of any particular tree for the full length of their development. A device has already been proposed (PAGE C.N., 1979) which to my experience also permits to preserve the purple pigmentation of immature cones intact for the herbarium, but I propose photography as another, additional efficient stratagem. The colour of cones collected before maturity but opening on drying is sometimes also indicative of immature colour, while that of open cones collected after maturity rarely is.

Yellow, or greenish female flowers of *Pinaceae*, sometimes tinged reddish, appear always to develop into green cones, while more or less dark purple, or violet flowers may either develop into green, or into violet/purple immature cones. Several closely related taxa in several genera of *Pinaceae* have, in fact, already been recognized as (slightly) differentiated sister-taxa, either based on colour-dimorphism (purple versus green) of immature female cones alone, and/or based on other/additional differences in external morphology. However, there are examples, where such a differentiation into separate taxa has not yet, or not convincingly been attempted. Some of these examples are recorded in the literature as intraspecific cone colour dimorphism (e.g. *Abies concolor* , STURGEON K.B. & al., 1980), but distinction must be made between this type (always purple versus always green coned taxa or populations), and other patterns of colour dimorphism (basically always green and, at times, more or less reddish coned species).

It has also remained unnoticed to the present that dimorphism in immature female cone colour in sister taxa (or sister populations within taxa) very often is accompanied by a similar dimorphism in the colour of male strobili ultimately before pollen release, an apparently very significant correlation. Among sister taxa (or sister populations) the taxon (or population) bearing the dark cones seems to consistently mature its seed earlier than its green coned kin, if grown side by side (e.g. *Pinus ponderosa* sensu lato of the Pacific Northwest versus variety *scopulorum* and Sierra Nevada western slope Ponderosa pine; *Pinus heldreichii* versus *P. nigra*, etc. ...). Purple coned taxa (populations) consistently grow in refugia, or at higher elevations, or in more northern latitudes, than their green coned sister taxa (populations).

Immature male and female cone colour, exact dates of cone-opening in diverse species,[1] and data on other correlated features in *Pinaceae* is poorly documented, as a rule; data on these subjects, with all the ambiguities inherent to such a procedure, either originates from own observation on both, herbarium material, and on individuals planted for ornament, or

TABLE 1: Distribution of immature female (and male) cone colour dimorphism among genera of Pinaceae and among areas (data as far as available).

Genus: Picea (1)

Area	Purple coned species		Actual, or putative green-coned sister-species (-population)	
	colour/male conelets prior to maturity			colour/male conelets prior to maturity
North America	red purple	P. breweriana		
Asia/North America (see also eastern Asia)	red	P. mariana		
	red	P. glehnii P. morrisonicola	P. rubens	red
	red purple	P. jezoensis	P. sitchensis	red
Eurasia		P. obovata (2)	P. abies var.acuminata var.abies (europea)	red
	red	P. omorika	P. orientalis	red
Eastern Asia (see also Asia/North America)		P. bicolor P. purpurea P. brachytyla var. complanata	P. brachytyla aggr., especially P. brachytyla var. brachytyla, P. wilsonii	
	purple	P. likiangensis var. balfouriana P. likiangensis var. rubescens P. montigena	P. likiangensis var. likiangensis	
		P. crassifolia P. meyeri	P. asperata	
		P. schrenkiana	P. smithiana P. spinulosa	yellow

Annotations

1) Since taxonomic relationships between species of Picea are still not very clear, it is particularly difficult in this genus to affiliate purple coned and their putative green coned sister-species.

2) P. obovata is predominantly Siberian but also occurs on some of the high Mountains of Central Europe (!!!). The sister-taxa P. obovata-P. abies sensu lato are perhaps another case exemplifying a conifer of which most, if not all, Cenozoic evolutionary stages may still be extant: Closure of the Tethys - seaway during the Oligocene, beginning continentality and seasonality of climate; evolution of vicariads (P. abies var. acuminata in the Carpathian Mts., a geologically old range, where it is still the prevalent taxon and P. abies var. (europea) abies in the European Alps). To confuse things even more the ancestor has survived to the present on some higher peaks in Central Europe (SCHMIDT-VOGT H., 1987). A similar sequence may have happened at the eastern edge of the area of Picea obovata. In eastern Asia P. koraiensis, P. pungsianensis etc..., are putative candidates for exemplifying similar evolutionary events.

3) P. orientalis is several times reported to have purple cones. However, it is the flowers that are purple, the young cones are always green.

TABLE 1: Distribution of immature female (and male) cone colour dimorphism among genera of Pinaceae and among areas (data as far as available).
(Contin.) **Genus: Abies and Keteleeria**

Area	Purple coned species		Actual, or putative green-coned sister-species (-population)	Annotations	
	colour/male conelets prior to maturity			colour/male conelets prior to maturity	
North America	reddish- purple bright red red or rose	*A. magnifica var. magnifica*	*A. magnifica var.shastensis* A. procera (1)	reddish-purple	1) Several authors describe the cones of A. procera as having purple scales entirely covered, however, by green bracts. Only LTU T.S. (1971) states A. procera possessing green cones *(perhaps meaning the green bracts ?)*. 2) In A. fraseri the purple scales are entirely covered by the green bracts. In this species (also in A. procera ?) the green bracts may achieve a function similar to that of green scales in other species.
		A. amabilis (purple as a rule)	A. amabilis (rarely green)		
		A. concolor var. concolor	A. concolor var. concolor A. concolor var. lowiana		
	red	A. religiosa A. hickeli A. vejari (both varieties)			
	reddish-purple	A. balsamea	A. fraseri (2)	yellow tinged red	
	dark blue	A. lasiocarpa var. lasiocarpa (purple as a rule) A. lasiocarpa var. arizonica	A. lasiocarpa var. lasiocarpa (rarely green)		
Siberia and eastern Asia		A. homolepis var. homolepis	A. homolepis var.umbellata A. holophylla	yellow	
		A. mariesii A. kawakamii			
		A. chensiensis var. ernestii	A. chensiensis var. chensiensis		
	scarlet	A. delavayi (all vars.) A. fargesii (all vars.) A. recurvata A. squamata			
		A. koreana	A. koreana		
	reddish	A. nephrolepis var. nephrolepis	A. nephrolepis var. chlorocarpa	greenish yell. or yell.red	
		A. sachalinensis var. sachalinensis	A. sachalinensis var. mayriana		
		A. veitchii var. veitchii	A. veitchii var. olivacea		
		A. veitchii var. sikokiana	A. veitchii var. sikokiana (A. Sikokiana var. olivacea)		
	yellow tinged red	A. sibirica var. sibirica	A. sibirica var. semenovii (?)		
		A. spectabilis A.pindrow			
Europe (only green cones in all taxa of Abies)		Keteleeria fortunei	Keteleeria davidiana		

TABLE 1: Distribution of immature female (and male) cone colour dimorphism among genera of Pinaceae and among areas (data as far as available)
(contin.) **Genus: Pinus (2)**

Area	Purple coned species		Actual, or putative green-coned sister-species (-population)		Annotations
	colour/male conelets prior to maturity			colour/male conelets prior to maturity	1) sometimes reported to have deep red cones, other instances reporting green cones. 2) Immature cone colour is particularly poorly documented in this genus, and the present enumeration probably very incomlete. 3) Green coned individuals of P. cembra are known from low elevations throughout the geographic range of the species in Central Europe (known in the past as var. helvetica CLAIRVILLE). The colour of cones of P. sibirica is not recorded anywhere.
		Ponderosa-complex			
North America	purple	P. ponderosa s.l.(Pacific Northwest)	P. ponderosa var.scopulorum	yellow-green	
	purple	P. washoensis	P. ponderosa (Sierra Nevada west-slope)	tinged red rose to red	
	orange to yellow	P. jeffreyi			
		Montezuma-complex			
		P. montezumae (several of its "forms", e.g.what in the past was known as P. gordoniana HARTWEG)	several other "forms" of P. montezumae		
		P. montezumae var. lindleyi			
		P. montezumae var. rudis			
		P. hartwegii			
		P. cooperi			
		P. michoacana (the "form" knwon in the past as P. russeliana LINDLEY)	P. michoacana (incl. var. cornuta ?)		
		Pseudostrobus-complex			
		P. pseudostrobus var. apulcensis			
		P. maximinoi (P. pseudostrobus var. tenuifolia)	several other "forms" of P. pseudostrobus		
		P. douglasiana			
		P. oaxacana (?)			
		Other Pinus-species			
	scarlet	P. albicaulis	P. flexilis	reddish	
	deep red	P. longaeva	P. aristata	yellow	
	dark orange-red	P. balfouriana ssp. austrina	P. balfouriana ssp.balfouriana (2)	yellow	
		P. resinosa (1)			
Eurasia		P. heldreichii	P. nigra	greenish-yellow	
		P. leucodermis			
		P. uncinata	P. sylvestris	yellow	
		P. pumilio (one of the"forms" of P.mugho)			
	purple	P. cembra	P. cembra (3)		
Eastern Asia	deep red	P. pumilio			
		P. massoniana s.l. ("forms" of ...)	P. massoniana s.l.		
		P. yunnanensis s.l.("forms" of, e.g. P. sinensis)	P. yunnanensis s.l.		

TABLE 1: Distribution of immature female (and male) cone colour dimorphism among genera of Pinaceae and among areas (data as far as available).

(contin.) **Genera: Larix, Pseudotsuga and Tsuga**

Area	Purple coned species		Actual, or putative green-coned sister-species (-population)		Annotations
	colour/male conelets prior to maturity			colour/male conelets prior to maturity	
Asia		L. griffithiana L. potaninii	L. mastersiana		
North America		L. lyallii	L. occidentalis		(purple bracts may have taken the role of purple scales)
Asia		P. japonica (?)			
North America		T. mertensiana T. crassifolia	T. heterophylla T. canadensis		

from scattered, and sometimes contradicting hints found in a diversity of manuals and must, therefore, be verified in every particular case mentioned here. The enumeration of purple coned species, and of putative pairs of taxa exhibiting colour dimorphism in *Pinaceae* (table 1) will, for the same reason, also be rather incomplete.

It is interesting to note from that compilation that purple coned species (populations), very often together with their actual, or putative green coned sister taxa (populations), are well represented in all larger genera of *Pinaceae* (although, interestingly, purple coned species appear, to my knowledge, to be absent in *Pinus*, subsection *strobi* LOUDON) and well distributed among both the Old, and the New World. Purple coned taxa (populations) are either concentrated in refugia, or increasing in numbers towards higher elevations or boreal latitudes. The number of species -pairs (purple and green coned sister taxa, or populations) is highest in middle latitudes, and decreases towards both, lower, and boreal latitudes. These patterns of representation among genera, and of geographic distribution, are too conspicuous to be without significance. An interpretation of this significance is attempted as follows:

Since purple pigmented female cones in *Pinaceae* are here considered to be primitive, an explanation for both, its probable function in Early Tertiary time, and, because many species exhibiting purple cones have survived to the present, the causes which have permitted their persistence, and coexistence in allo-, and/or para-, and/or even sympatry with green coned species must be sought for. In addition to that, any notion of the pressures probably responsible for Middle Tertiary evolutionary change, and of the effect of this change (towards cones pigmented green) must also be brought into congruence with the other causes.

The ecological role of anthocyanin pigmentation of plant-parts has only rarely been comprehensively discussed previously (e.g. McCLURE J.W., 1975). The functions of these pigments possibly playing a role in conifers in general, and in *Abies concolor* in particular, have more recently been reviewed by STURGEON K.B. & al. (1980). Two of their lines of reasoning deserve additional discussion here. They have already pointed out, and their reasoning is strongly supported by the data compiled in this manuscript, that screening against UV-radiation must definitely be discarded now as function of purple pigmentation in conifer-cones at high elevations, since radiation increases with elevation and decreasing latitude, while the frequency of purple cones (and of purple coned species, as enumerated in this paper) increases with altitude, but, contrary to radiation, also with increasing latitude.

Their other finding concerns the thermoregulatory function of the purple colour. Pigmented cones (in *Abies concolor*, but certainly also in other purple coned *Pinaceae*) attain higher internal temperatures than do green cones (see also McCLURE J.W., 1975, p.1018: "... anthocyanins and other flavonoids may play a role in alpine and northern regions by absorbing light and warming the tissues ..."). STURGEON K.B. & al. suggest that dark purple cones may represent an adaptation to higher elevations, because higher internal temperatures may have a positive effect on seed-set, and seed-maturation. This reasoning is certainly correct for *Abies concolor* (and purple coned *Pinaceae* in general), but probably represents only part of the truth, since "... in addition to Colorado and New Mexico, white fir is also found at high elevations in Utah, Nevada, and southern California ..." but "the purple variant is not present at these sites" (STURGEON K.B. & al., 1980). If, however, the thermoregulatory function is reconsidered, again in the context of the probable general Cenozoic paleohistory of North American vegetation, such inconsistencies appear to be resolvable. Early Tertiary climate, as discussed in earlier paragraphs, was, in the main, characterized by equability (narrow ranges of temperature extremes, general absence of either pronounced hot, or precisely cold seasons), although areas in uplands experiencing equable, but relatively (relative to the general, latitudinal climate) low temperatures have enabled boreal taxa (e.g. *Pinaceae*) to migrate from North to South, and to reach low latitudes as early as Upper Cretaceous (e.g. Mexico, RZEDOWSKI J., 1978, p.91). Reproduction (the germination of seeds) in Early Tertiary *Pinaceae* appears, therefore, not to have been hampered by these relatively low, but equable temperatures (I have several times observed species of *Abies* to germinate under snow).

But, another pattern of seasonality appears to have accompanied the early evolution of *Pinus* (and of *Pinaceae*, all of which were of northern origin): More or less pronounced wetter, and dryer seasons (MIROV N.T., 1967, p.571). Pines, for example, grow, but do not reproduce "in ever wet, and uniformly hot climate; for their normal development they require ... either dry and wet, or warm and cold seasons, often a combination of both types" (MIROV N.T., l.c.). It can be assumed with a high degree of certainity that vegetative development was, in the main, restricted to the wetter, and the development of reproductive organs to the dormant dryer (warmer) season in a montane, relatively cool Early Tertiary environment. Even today, vegetative development in conifers is, in the main, restricted to several weeks in the wet, and in a cool season, where these characteristics coincide. In many conifers vegetative development is resumed after a dormant, dry season, but the reproductive organs nevertheless develop and ripen during this dormant, but warm period. Such a background may have induced Early Tertiary *Pinaceae* in an equable, ever cool montane environment, to evolve anthocyanin pigmentation of their female reproductive organs to absorb more warmth and to contribute in such a way to the timely ripening of their cones to the onset of the wetter season. The alternative interpretation, anthocyanin pigmentation to accumulate warmth during the wetter season, would not be consistent with all other data on the physiology, reproductive behaviour, and paleohistory of *Pinaceae*. Also today do purple coned species ripen their female reproductive organs in the dry season (when vegetative development is dormant), and if grown side by side with their green coned sister-taxa, consistently shed their seeds earlier by several weeks; these would certainly germinate soon, if temperatures remained higher at the onset of the wetter winter-season (Early Tertiary temperatures are considered to have been higher than those at present). A cool, but equable Early Tertiary climate is likely not to have hampered the survival and permanent establishment of seedlings. However, a Later Tertiary climatic deterioration completely altered these circumstances.

The Oligocene convincingly is said to have seen the initial development of a pronounced seasonal climate with regard to temperature (higher ranges of temperature extremes, pronounced continentality of climate in the interior of continents, and freezing winter temperatures also at middle latitudes), thus outweighing the effects of seasonality of climate solely related to available humidity, and in such a way contributing to a deterioration of adaptation in many taxa (e.g. *Pinaceae*) having been termed "Oligocene Crisis" by one author (AXELROD D.I., 1987), and "Terminal Eocene Event" by another (WOLFE J.A., 1978). Seedlings of *Pinaceae* probably adapted to emerge from seeds practically immediately upon seed-release of cones (I have observed seeds of *Pinus flexilis* collected from the ground under the tree on August 6, to germinate three weeks later if brought immediately into the seed-bed), were now exposed to increasing extremes of low (winter) temperatures deleterious to their survival and permanent establishment. *Pinaceae* had, therefore, to rapidly (perhaps 1 to 2 Ma, see WOLFE J.A., 1978) evolve a mechanism to overcome the threat; since the loss of an adaptation is easier to evolve than to gain one, they appear to have chosen one or two strategies out of the mechanisms they were preadapted to: loss of purple pigmentation in reproductive organs (e.g. in *Pinus cembra*, and perhaps also in other species, the potential to develop green-coned "mutants" is still extant, see table 1), and/or, perhaps simultaneously in some cases and not in others, proliferation of the ability of their seeds to postpone germination by dormancy. The main mechanism at low to middle latitudes and at lower altitudes, loss of purple pigmentation in female reproductive organs of *Pinaceae* postponed the ripening of their seeds well into the cold season when temperatures were already low enough to prohibit their premature germination. Vicariance of populations may have been crucial to enhance evolutionary change towards green cones in some cases, and seed dormancy may have assisted in the effect of postponing premature germination of seeds in other cases. In more northern latitudes and at higher altitudes both, overall summer- and winter-temperatures may have significantly dropped in the Oligocene; lower summer-temperatures may have counterbalanced the effect of purple pigmentation of cones to accumulate warmth, with consequences similar to those of evolving green cones at lower latitudes.

Circumstances as these may perhaps convincingly explain both, the evolution of green coned sister-species in the Oligocene, and the persistence to the present of their purple coned ancestors in many instances. The lower the altitude, or the latitude, the more taxa appear to have been compelled to evolve green coned vicariads (populations) to postpone seed-ripening; and conversely, the higher the altitude, or the latitude, the less purple coned species of the conservative *Pinaceae* were forced to evolve strategies against premature ripening of their female reproductive organs. And green coned *Pinaceae* predominate, in fact, at low latitudes and at lower altitudes; pairs of bimorph sister-taxa (populations) increase in numbers from low to middle latitudes (and higher altitudes); and purple coned *Pinaceae* generally predominate at high latitudes, with the exception of some pioneer species in several genera which appear to have extended their geographical ranges to boreal latitudes very recently (Quaternary, see MIROV N.T., 1967, for *Pinus*, e.g. *P. banksiana*, *P. contorta*, *P. sylvestris*, etc. ...). These recently immigrated boreal green coned species show no tendency towards purple pigmentation of cones, thus corroborating the view that the change from purple to green pigmentation obviously was a necessity at a particular climatic transition (perhaps 1 to 1,5 Ma, see WOLFE J.A., 1978) in the past, a paleoclimatic constraint particularly effective at low and middle latitudes, but having been (and still being) insignificant at high latitudes, where lowered warm season temperatures may have been similarly effective.

The geographical range of purple coned taxa of *Pinaceae* at middle latitudes always appears to be restricted to (montane) refugia distinguished by a relatively milder and more equable climate (or where their other specific requirements, e.g. a minimum of summer-precipitation, can still be met with) as compared to the environment with more severe continental climate in which their green coned sister-taxa (populations) thrive. The modern pattern of distribution of these bimorph sister-taxa in western North America appears always to reflect the Tertiary trends of change in the vegetation of this continent in general. Purple pigmentation of cones in all species (populations) of all *Pinaceae* is genetically fixed and not variable according to environmental factors (see discussion of this aspect in STURGEON K.B. & al., 1980). All individuals of either purple coned, or green coned *Pinaceae* retain their cone colour if transplanted to environments theoretically advantageous to the other colour.

It must be stressed, however, that the presence of purple pigmentation in cones of *Pinus* (and *Pinaceae*) solely suggests that the particular genotype has retained this particular Early Tertiary adaptation unchanged to the present, but may of course have become more advanced since then in several other characteristics. Conversely, species (populations) now exhibiting green cones were at one time compelled to adapt one particular characteristic to a changing climate, but may have remained primitive in several other features. However, documented recognition of sister-taxa, bimorph in immature cone colour and in several cases also differentiated (although practically always only slightly) in other respects, and on the other hand, the genetical integrity maintained by bimorph sympatric green and purple coned phenotypes (populations) apparently not showing additional discernible morphological differentiation in other respects indicates that purple and green coned genotypes are genetically already well differentiated.

Apart from presumed introgression between "cone colour-variants" in *Pinus ponderosa* s.l. in the Pacific Northwest (see above for an alternative explanation), no other hybridization phenomena (perhaps with the exception of single intermediate individuals in some cases) between green and purple coned sister-taxa (populations) have so far been reported. Behaviour in hybridization experiments, as reported in a multitude of papers by W.B. CRITCHFIELD, and coworkers, appears, moreover, to indicate that modern purple coned taxa are still quite closely related to their Early Tertiary kins, more so than their Oligocene primary, and (where such have evolved) much more so than their Pliocene secondary vicariads, although the relative phylogenetic age of any particular green coned sister-taxon (population) can at present only be assessed in the context of probable paleogeologic events and paleoclimatic trends in any particular region.

The four diagrams in figure 1 aim at demonstrating the probable mutual relationships of purple coned genotypes, and of their vicariads exhibiting green cones, among some taxa, or "groups" of *Pinus*. Further subdivision of "groups" has been avoided in some cases (e.g. *Australes*), and some diagrams are somewhat oversimplified in other respects solely for the sake of clarity. The hybridization-behaviour of these taxa (populations) of *Pinus* (in some cases already alluded to in earlier paragraphs) illustrates the (probable or factual) correlation of the pigmentation of immature female cones to retained crossability (as exhibited among Early Tertiary purple coned taxa within subsections of the genus, and between purple coned taxa and their direct Middle or Late Tertiary offspring/vicariad), and to acquired genetic distance (as exhibited among green coned taxa or populations, and between purple coned taxa and green coned vicariads of different parentage).

Among *Australes* and *Ponderosae*, Sierra Nevada western slope Ponderosa pine (secondary vicariad), and *Pinus washoensis* (one purple coned paleorelict and taxon more or less controversially accepted among the "races" of *Pinus ponderosa* s.l. in the Pacific Northwest), have experimentally shown each to be more closely related to variety scopulorum (primary vicariad), than to one another (CRITCHFIELD W.B., 1984; see also paragraph 4). Virtually all attempts to cross Sierra Nevada western slope Ponderosa pine (secondary vicariad) with any of the taxa (primary vicariads of different parentage) comprising the group "*Australes* " have failed (CRITCHFELD W.B. 1963a; see also paragraphs 2 and 4). These results and the relationships suggested in figure 1 appear to corroborate each other.

All attempts but one to cross *Pinus resinosa* and *Pinus nigra* have so far

Figure 1: Diagrammatic model to demonstrate probable relationships among "groups" ("species") of *Pinus* Australes / *Ponderosae* (*Sabinianae*)

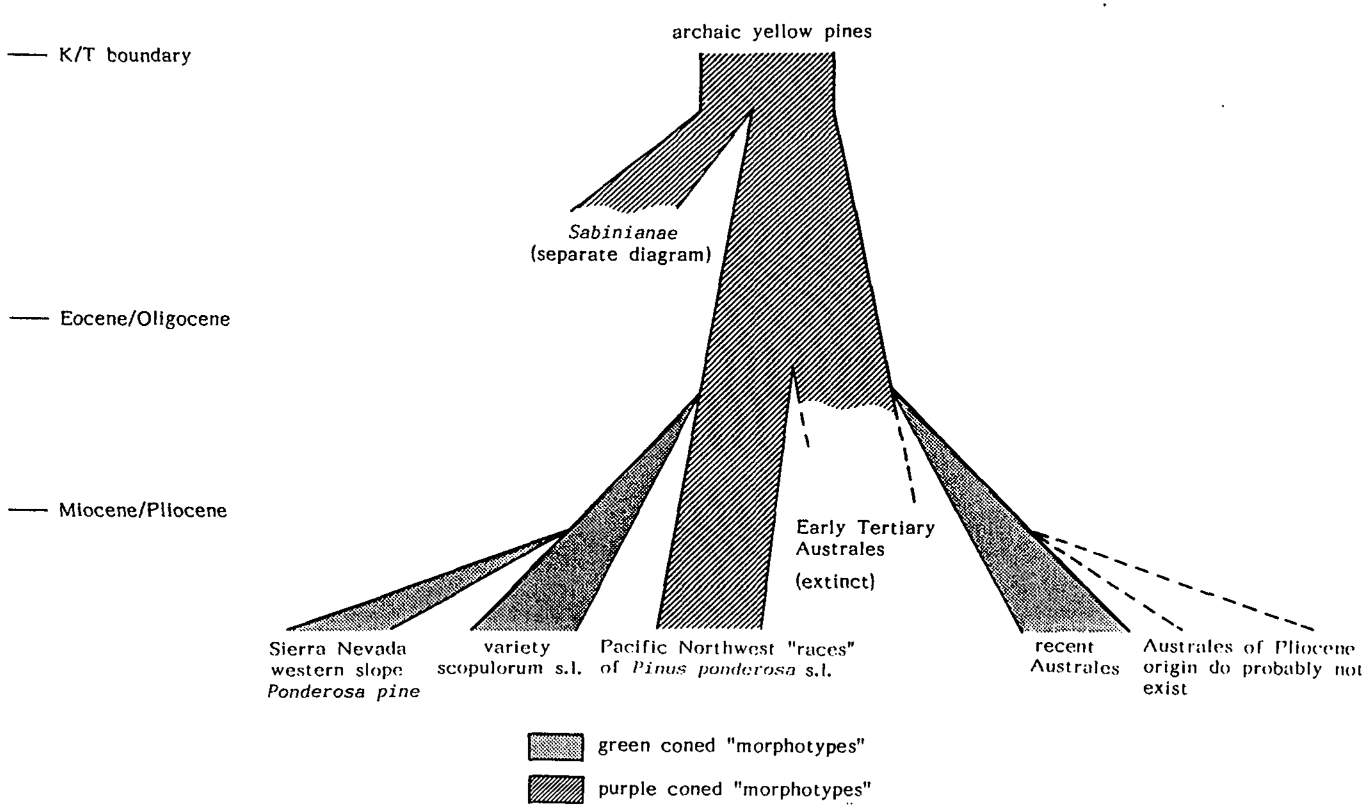


Figure 1: (continued)

Diagrammatic model to demonstrate probable relationships among "groups" ("species") of *Pinus*

Black pines

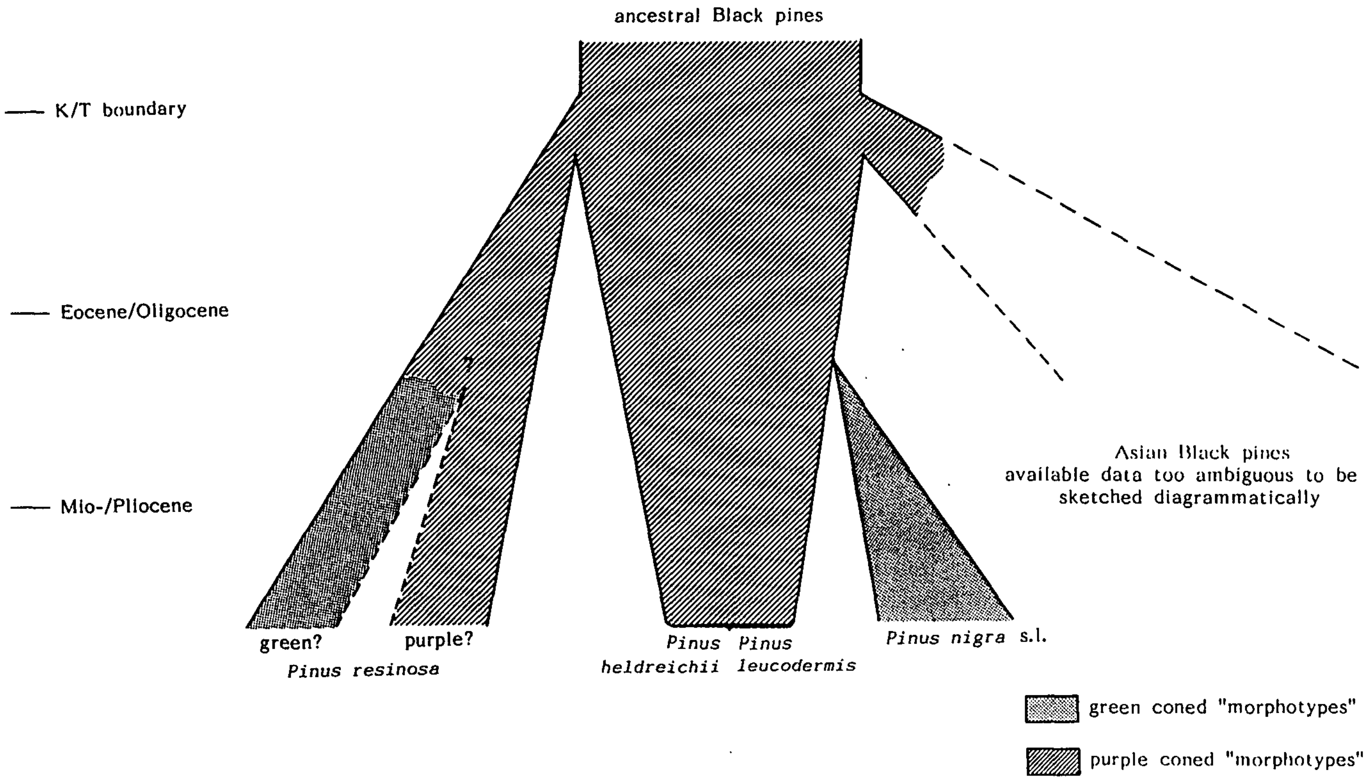
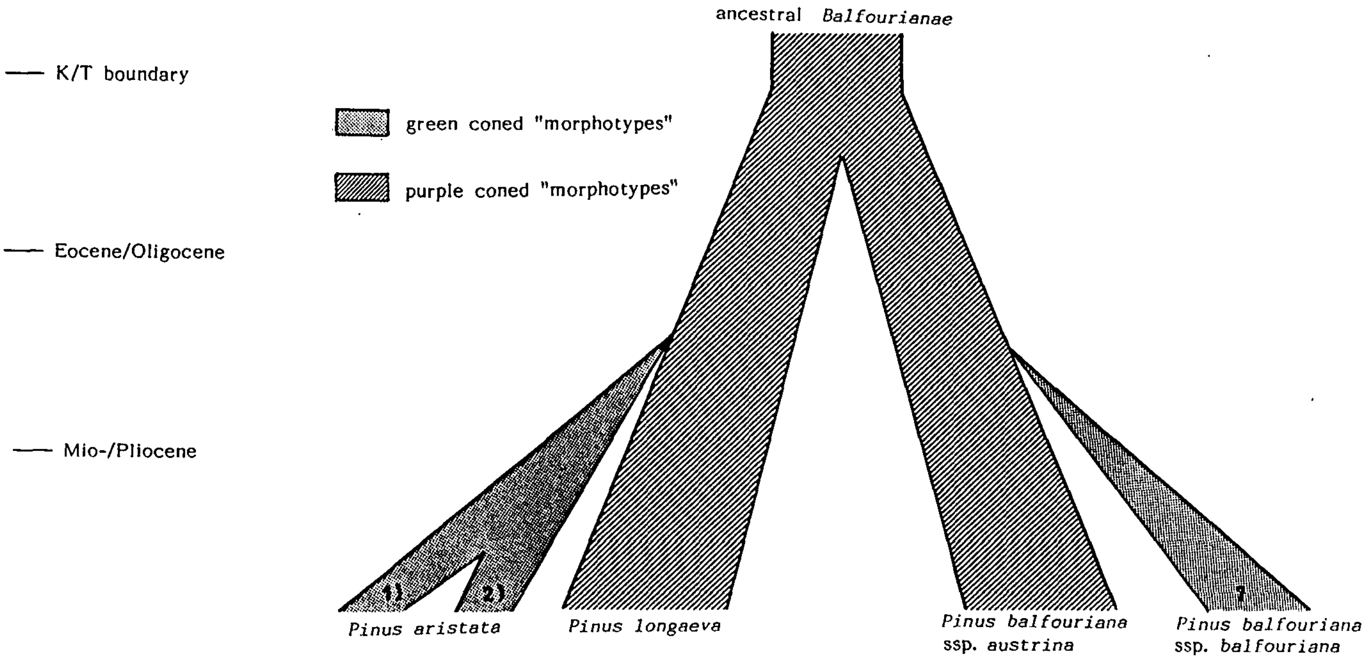


Figure 1: (continued)

Diagrammatic model to demonstrate probable relationships among "groups" ("species") of *Pinus*

Balfourianae

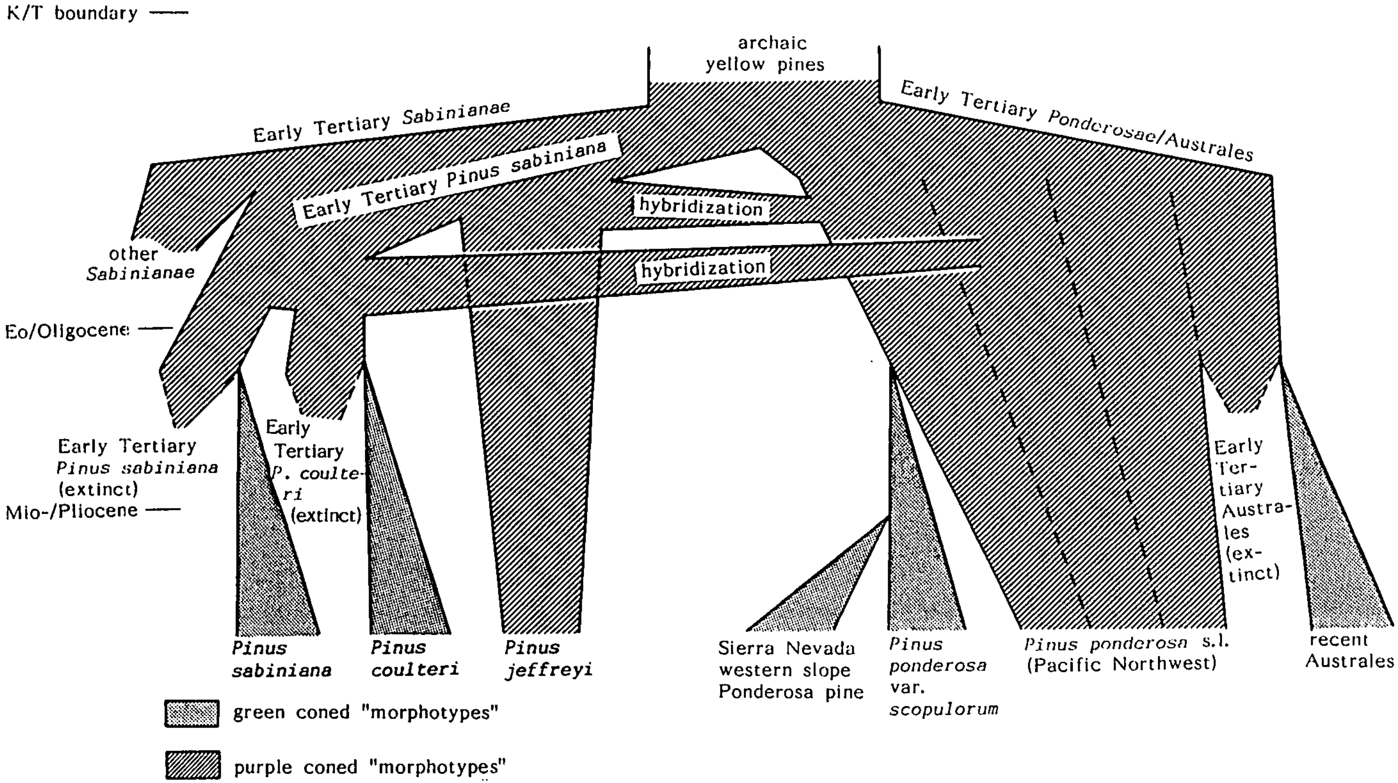


1) Populations East of the Colorado River
2) Green coned individuals among populations of *Pinus longaeva* West of the Colorado River

Figure 1: (continued)

Diagrammatic model to demonstrate probable relationships among "groups" ("species") of *Pinus*

Sabinianae/Ponderosa-complex (Australes)



failed. The one successful attempt yielded a very small number of putative hybrids, and pollen contamination was probably involved (CRITCHFIELD W.B., 1963b). Some manuals report immature cones of *Pinus resinosa* to be green, others show them to be purble. The correct colour ought to be green according to own observation. However, regardless of actual immature colour, whether the recent *Pinus resinosa* still possesses its Early Tertiary (purple coned) genotype, or rather is of Oligocene origin (green cones), red pine probably is more closely related to *Pinus heldreichii* , or to *P. leucodermis* (both exhibit the ancestral purple immature cone colour), than to *P. nigra* , the green coned obvious vicariad of the former (different parentage). Attempts to hybridize *P. resinosa* probably ought, therefore, to be carried out with *P. heldreichii* and *P. leucodermis*.

Geographically remote populations of both, bristle cone, and foxtail pines, more recently, have each been split into two separate taxa: Bristle cone pine into *Pinus aristata* (green cones) east of the Colorado River, and *P. longaeva* (purple cones, with some green coned individuals at lower elevations) on high plateaus west of the Colorado River; and foxtail pine into *Pinus balfouriana* ssp. *balfouriana* (northern population in the Klamath Region; immature cone colour is not explicitely stated, although other data indicates that it may be green), and ssp. *austrina* (southern populations with purple immature cones on high peaks in the Sierra Nevada). The subspecies of *Pinus balfouriana* are easily crossed with one another as could be expected. But also the low crossability of ssp. *balfouriana* (probable vicariad of ssp. austrina) with *P. longaeva* (probable ancestor of *P. aristata*), and the full crossability exhibited by *P. balfouriana* ssp. *austrina* and *P. longaeva* (both purple coned and probably of monophyletic Early Tertiary origin), a circumstance so much wondered at (CRITCHFIELD W.B., 1977), are fully consistent with the hypothesis presented here and diagrammatically shown in figure 1. The western populations of green coned *Pinus aristata* are postulated to have become disjunct from the populations east of the Colorado River in the Pleistocene; too little is known of the populations of bristle cone pine in Arizona to adequately represent them in the diagram.

The relationships among *Australes/Ponderosa*-complex and *Sabinianae* may be as complex as suggested in figure 1. The limited compatibility exhibited by several of the crosses attempted so far (CRITCHFIELD W.B., 1966; see also paragraph 2) appears to generally conform to this arrangement.

Crosses between *Pinus coulteri* and *P. jeffreyi* are easier to perform than crosses between *P. coulteri* and *P. sabiniana*, a circumstance consistent with the probable relationships as shown in the diagram: The latter appear to be genetically more distant already from one another than either of them from *P. jeffreyi*. An yet inexplicable inconsistency is hidden in the fact that crosses between *Pinus sabiniana* and *P. jeffreyi* were less successful than crosses between *P. coulteri* and *P. jeffreyi*. Additional tests ought to be carried out to clarify these relationships more comprehensively (several reciprocal crosses have not yet been attempted).

It is beyond the scope of this manuscript to also discuss several other implications inherent to the thesis on the significance of pigmentation of immature female cones of *Pinus* and other pinaceous genera.

7. Attempt at formulating a taxonomic concept applicable to the *Ponderosae* (to *Pinus* and *Pinaceae* in general)

The combined consideration of conclusions reached by a multitude of workers in paleobotanical studies of *Pinaceae* (see Introduction), and of studies resulting in the formulation of a convincing general concept of Tertiary development and change in North American vegetation (see paragraph on "Paleontological setting") permit to tentatively suggest that pronounced evolutionary conservativism has restricted Cenozoic evolutionary innovation in *Pinus* (and *Pinaceae* in general, see "Introduction", and also WRIGHT J.W., 1955, p.344), and especially the evolution of new genotypes with concomitant development of at least slightly divergent morphological characters, to only a very few instances of either

1) evolutionary occasions: Decline of the Mesozoic plant world at the K/T-Transition, which particularly affected the vegetation at middle latitudes (WOLFE J.A., 1987a; and 1987b); the diversity of new microhabitats additionally opened to colonization by plants concomitant with extensive Early Tertiary volcanism, and Laramide orogeny (AXELROD D.I., 1981; WOLFE J.A., 1987b); a plant world still much in desequilibrum all through the Early Tertiary, e.g. the Early Eocene thermal maximum (WOLFE J.A., 1987b); and, towards the close of the Tertiary, again local mountain building in, among several regions, the area of the present Sierra Nevada in California, where at the same time a mediterranean type of climate was developing (AXELROD D.I., 1959); or

2) evolutionary constraints (Oligocene initiation of pronouced temperature related seasonality, and also of continentality of climate due to the regression of epicontinental seaways in the interior of continents (factors which have contributed to the "terminal Eocene event", or the "Oligocene crisis", as circumscribed by AXELROD D.I., 1986; AXELROD D.I., 1987; WOLFE J.A., 1978).

The Late Tertiary major climatic deterioration, however, the incipient short term climatic oscillations, although occurring concomitant with a decline in diversity among the boreal floras, did not act as similar, major constraint to evolve new genotypes (HUNTLEY B. & al., 1989; SPAULDING W.G., 1984): Ecotypes/genotypes of *Pinaceae* adapted to continentality and temperature related seasonality of climate had already evolved concomitant with the "Oligocene crisis"!.

The probable evolutionary burst initiated in *Pinus* (and also the *Pinaceae*) around the K/T-transition may have initiated the prolific splitting of "archaic" (no more extant?) "Haploxylon" and "Diploxylon" taxa of pine (which may be considered to have been at the origin of the infrageneric groupings in their present circumscription, see AXELROD D.I., 1986, p.570, fig.2), thus creating an array of partly still existing, ecologically distinct, and morphologically more or less well differentiated offspring. This ancient offspring appears the better perceptibly differentiated today, the steeper the ecological gradient had been into which these Early Tertiary ecotypes evolved, and consequently, depending on the magnitude of the morphological gaps separating this ancient, but surviving diversity today: The comparatively slight, but nevertheless easily perceptible morphological differences between the bristle cone pines and foxtail pine on the one hand, and the continuum of diversity presumably exhibited by an aggregate of "morphotypes" of *Pinus ponderosa* sensu lato in the Northwest on the other hand, may represent a good example to illustrate this line of thought. Similar correlations between original Early Tertiary magnitude of diversitv surviving to the present, and easiness to perceive taxa today are apparently also evident in other *Pinaceae* (e.g. in *Picea*, see WRIGHT J.W., 1955). Where this Early Tertiary offspring in *Pinus* and other *Pinaceae* have seemingly survived to the present, their component taxa (or populations) seem to exhibit one common characteristic: purple immature female cone colour (this feature is perhaps absent in true white pines?); here, the term "populations" refers to examples in several genera of *Pinaceae* where former taxonomic concepts have not, or not yet permitted the perception of distinctive taxa in those cases where "morphotypes" of apparently Early (purple coned), and later Tertiary origin (green coned) occur in association, e.g. "variants" in cone colour of *Abies concolor* as only one of a multitude of existing examples (see paragraph 6). In general, the recognition of taxa would not pose problems to taxonomists today if purple coned presumable Early Tertiary ancestors were considered alone. However, the coexistence of these "variants" adds to the taxonomic complexity encountered in many modern conifers.

The modern purple coned taxa (or populations) are, of course, not genetically identical to their Early Tertiary kin, but they appear to have accumulated very little genetic change since the Paleogene, or in approximately 40 to 50 Ma, and are in most respects still very similar to their Early Tertiary progenitors, since they have apparently also retained the ability to the present to hybridize with their Early Tertiary sister taxa of common stock (e.g. *Pinus longaeva* / *P. balfouriana* ssp. *austrina*, see paragraph No 6). An adequate taxonomic reconnoissance of the yellow pines of North America, and probably of all other "difficult" groups of *Pinaceae* as well, ought, therefore, to begin with these putative oldest extant (purple coned) evolutionary genotypes of their respective groups. In the yellow pines it is the "morphotypes" surviving in the Pacific Northwest, or North Plateau which appear to represent the most complete still existing assemblage of genealogically oldest, but poorly surveyed yellow pine genotypes.

All these Early Tertiary taxa (the yellow pines among them) have migrated from North to South, and many of them also from West to East on the continent of North America, colonizing their particular ecological niches over wide middle latitude areas encompassing also ancient highlands in the area of present Mexico (Eurasian taxa of *Pinus* appear to have experienced a similar history, although migration is likely to have occurred from East to West on these continents, see MIROV N.T., 1967).

Middle Tertiary incipient aridity in the interior of continents has progressively split the vast territory of these Early Tertiary taxa. They were progressively restricted to increasingly smaller and, where still extant, into at present relictual areas which are even today characterized by a generally more equable climate. Taxa of *Pinaceae* of obviously Early Tertiary origin, and occupying large areas today, are without exception restricted to taxa at high, boreal latitudes (e.g. *Picea obovata, P. mariana, Abies sibirica, Pinus cembra sibirica* (?), etc. ...), to areas they have been able to colonize in the recent (Holocene!) past (MIROV N.T., 1967) since, due to changed climatic parameters, the evolutionary retainment of purple pigmentation of cones is not deleterious anymore to their successful reproduction and, therefore, to their survival in this severe climate today (see paragraph No 6).

Besides incipient aridity, the interior of northern hemisphere continents was also experiencing Middle Tertiary incipient temperature related seasonality, and also intensifying continentality of climate. These additional climatic constraints (resulting in the "Oligocene crisis") appear to have acted on vicariating populations of these retreating Early Tertiary taxa to rapidly evolve ecological adaptations to the worsening climatic parameters. It is conceivable in particular cases that continuing deterioration of climate has in turn also split Middle Tertiary areas of distribution of these vicariads. And finally, Late Tertiary local orogeny, and locally developing mediterranean type of climate again induced only ecological adaptation in populations particularly exposed to specifically changing environments (secondary vicariads). These modes of speciation in *Pinaceae* , Early Tertiary adaptive radiation, and Middle and Later Tertiary vicariation, appear not only to be corroborated by the probable Tertiary general history of North American vegetation, but also to be well exemplified by the pattern of distribution and the pattern of diversity exhibited by the yellow pines of North America: An array of taxonomically yet imperceptible "morphotypes" and its pattern of diversity (similarities and morphological gaps) in the Northwest is paralleled by similar patterns of diversity in the Cordilleran Region (taxonomically slightly better perceptible), and again in the southeastern United States (already perceptibly differentiated "*Australes*"). This parallelism is certainly also evident in the Mexican yellow pines, but its recognition is complicated by the far greater diversity of yellow pines existing in this area.

Therefore, while dispersal, or adaptive radiation, appears to have been the effective mode of speciation in Early Tertiary, vicariance probably became the dominant pattern leading to differentiation in *Pinus* (and in *Pinaceae* as well) in the Oligocene, and in particular cases again in the Pliocene. These only few probable incidences of diversification, and the nature and amplitude of past evolutionary opportunities and/or constraints necessary to trigger them suggest that macroevolutionary change in phenotypic expression is not likely to be a factor in *Pinus* (or the *Pinaceae*) today (see Introduction), although it would be premature to completely exclude the possibility of recent evolutionary phenomena occurring in "difficult" groups of *Pinus* in poorly known areas, such as the Mexican Highlands, or Eastern Asia.

So, in spite of all these vicariation events, and in spite of the very extensive Early Tertiary evolutionary opportunities and Later Tertiary constraints distributed over a span of time of approximately 25 to 30 Ma since the "Oligocene crisis", or even longer, evolutionary development of distinguishing external morphological characters in *Pinus* (and the *Pinaceae*) was comparatively meagre only. Although microevolutionary genetic change may have continued to accumulate, this very change was not followed by a concomitant change in phenotypic expression. And, in fact, practically all genotypes of *Pinus* (and *Pinaceae*) of Middle to Late Cenozoic origin appear to have evolved only almost imperceptibly in time, and exhibit today characters of external morphology ranging from comparatively slightly divergent only, to almost indistinguishable, if standard taxonomic characters only are compared to the standard botanical characters of their immediate Early Tertiary ancestors. One characteristic apparently common to all genotypes of *Pinus* (and *Pinaceae*) having evolved in Middle to Late Tertiary time is the loss of purple pigmentation of their immature female cones. Some purple coned, and their green coned sister-"morphotypes" are so much similar in most external aspects thus simulating to the only casually observing taxonomist that evolutionary development in these divergent "morphotypes" was restricted to a change in immature cone colour only, from purple to green. However, visually not perceptible genetic change may have become of a magnitude already which complicates, or even prevents successful hybridization today. Such a development is exemplified by the genetic distance already acquired by the "morphotypes" of *Pinus ponderosa* var. *scopulorum* from their probable ancestors in the Northwest (see CONKLE M.T. & al., 1988; CRITCHFIELD W.B., 1984). All these Later Tertiary vicariads in *Pinaceae* appear to exhibit exclusively green immature cones which contrast to the purple cones of pinaceous taxa of obviously Early Tertiary origin. The green coned "variants" in *Pinus* (and *Pinaceae*) appear most often to thrive in a more continental type of climate as compared to the relictual areas of many purple coned "variants" which are most often characterized by a generally more equable climate. In (western) North America the modern distribution of purple, and green coned "variants" of taxa (populations) of a variety of genera of *Pinaceae* appear to be well correlated to past climatic change and the probable Tertiary general history of vegetation of the continent: Several examples have been discussed in the preceding paragraphs. The Middle Tertiary vicariads in *Pinus* are also characterized by their differential behaviour to cross with their closest relatives: These vicariads appear to be crossable to their immediate ancestors as could be expected (although they keep genetic integrity in parapatry), but these vicariads are very often not crossable anymore to their "cousin"-, or their "nephew"-taxa of comparable evolutionary history and age (contrary to the combination *Pinus longaeva/P. balfouriana* ssp. *austrina* , the alternative combination *Pinus aristata / P. balfouriana* ssp. *austrina* appears to have already become genetically incompatible, see paragraph No 6 for a detailed discussion and other examples). Similar to morphological diversification, it is apparently not long periods of geologic time which have induced genetic incompatibility in vicariating populations of *Pinus*; genetic incompatibility in this genus appears to be an expression of grade, or distance of relatedness of divergent, vicariating genotypes as represented by their probable relative position on the phylogenetic tree. Therefore, it is the genealogically younger vicariads which appear to have already become genetically incompatible to one another in many cases. Their ancestors, although already separated for much longer periods of geologic time, appear to have retained their ability to cross.

The multitude of "difficult" groups, of "aggregates" of *Pinaceae* composed of taxa of controversial taxonomic status testifies to the paucity of the evolutionary change in phenotypic expression induced in this gymnospermous group during long periods of geologic time and by a diversity of Tertiary forcing factors as mentioned above: The *Pinus mugho/P. uncinata/P. sylvestris*-complex (MIROV N.T., 1967), the *Picea obovata / P. abies*-complex (including also several Asian taxa of *Picea*, see SCHMIDT-VOGT H., 1987; WRIGHT J.W., 1955, p.342-346), several other complexes of *Pinaceae* in eastern Asia and in North America (e.g. the yellow pines, etc. ...), or complex groups in the genus *Abies*, the various classifications of which do also not correspond in several important particulars (LIU T.-S., 1971).

In order to perceive taxonomic units in *Pinus* (and other *Pinaceae*) more clearly, and to achieve a convincing infrageneric systematic arrangement it is necessary, therefore, to extend taxonomic considerations to additional, complementary botanical characteristics exhibited in the field, but also to results of studies in other botanical fields (e.g. paleohistorical, ecological, biochemical, anatomical studies, etc. ...). Reciprocally it would be very desirable if workers in related botanical fields would not blindly rely on conclusions reached by taxonomists and would consistently record as much data as possible on the origin and the external botanical characters of the plants sampled to carry out their experiments, especially of samples of taxa in "difficult" groups, e.g. *Pinus ponderosa* sensu lato, or the yellow pines in general.

In many "difficult" groups of *Pinaceae* , including the yellow pines of North America, several Early Tertiary ancestor-genotypes (where still extant), and the primary, and in a few cases secondary vicariads coexist today in allo-, and/or para-, and/or sympatry, thus contributing to their taxonomic complexity. Ancestors and vicariads must be seen as coexisting divergent "generations" of one and the same genome. The yellow pines of North America appear to have experienced prolific Early Tertiary speciation. These taxa have first been split spatially, and their component segments were then at the origin of Middle Tertiary primary vicariads, with some of the latter having given rise to secondary vicariads in the Neogene. Therefore, for the sake of a clear systematic arrangement, this large group of yellow pines must be subdivided into distinct phylads, the components of which were either split spatially, and/or have repeatedly, and consecutively vicariated in time into in many cases coexisting genotypes representing successively evolved "generations" of one ancestral genome. The systematic arrangement into phylads must clearly reflect this three-dimensional pattern of evolution of yellow pines in space and time as elaborated in this tentatively proposed concept. The heptane pines (see paragraph No 2) constitute, by the mode of their origin (differentiated biochemically, and not only ecologically), an independent, particular phylad of yellow pines which has otherwise experienced a Cenozoic evolutionary history very similar to that of the other yellow pine-phylads, of other taxa of *Pinus*, and other *Pinaceae*.

Epilogue

In several instances additional, genuine evidence would be highly desirable to corroborate the new lines of thought discussed here. However, it must be kept in mind that many studies to which the present discussion refers, were carried out basing upon wholly erroneous premises, on misconceptions as outlined in this manuscript. It is the inconsistencies hidden in these more or less fragmentary, although quite thorough studies, together with genuine evidence in many cases, which form the foundation on which the present alternative lines of thought rest. The choice of species of *Pinus* selected by KARALAMANGALA R. & al. (1989) for their electrophoretic study of relationships among *Ponderosae*, and some of the results (see paragraph 2), represent one typical example among many, many others: They spared no efforts to get truly authentic material from as far as the Mexican Highlands; however, since current ideas virtually negate a closer relationship between *Australes* and *Ponderosae* , none of the southern pines were included in the study, and the "crucial" evidence is, therefore, still lacking. A wealth of similarly incomplete results hiding, rather than disclosing true relationships is scattered in a multitude of the references cited in this manuscript. These sentences do not mean to criticize, but aim at highlighting the nature of the deficiencies encountered in attempting to corroborate the present new lines of thought. Moreover, the hints bearing on the present concepts are so numerous, and scattered in hundreds of references relating to taxonomy, ecology, forestry, plant geography, genetics, paleobotany, etc., and intricately related in a measure, which, for the sake of clarity and brevity, prohibits their combined discussion in a single manuscript.

Pinus ponderosa and the *Ponderosae*, their taxonomy and nomenclature are all no more than a colossal, Herculean chaos. These "taxa", their true identity, their general circumscription, their very nature, appear, in fact, to still be virtually obscure to all who have carried out studies in them. The present discussion perhaps helps to evaluate why, and how much of our current ideas on *Pinus ponderosa*, its complex, and the *Ponderosae* have simply to be thrown over board. We have to start again from point "zero". More detailed elaboration of yellow pine taxonomy must, therefore, be postponed till the *Ponderosae* are better understood conceptually.

In order to provide the new point of departure virtually necessary to truly promote progress in the yellow pines (including prevention of further cluttering the literature and indices with new names, or new combinations doomed to remain ephemeral), it was thought advisable to discuss the matter as it has been done here.

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