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The taxonomic status of *Pinus washoensis* H.MASON & STOCKW. (Pinaceae)

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Abstract

As one side result of a recently completed study, *Pinus washoensis* H.MASON & STOCKW. was found to be identical (conspecific) with *P. ponderosa* DOUGLAS ex C.LAWSON s.str. ('North Plateau race' of *P. ponderosa* var. *ponderosa* in its current circumscription). This conclusion not only contradicts the taxonomic opinion held by many other authors; the 'mythical' Washoe pine moreover continues to be believed rare and a matter of concern for conservationists. It thus seems appropriate to present, not only the technical taxonomic evidence pertaining to *P. washoensis* and its relegation into synonymy, but also a comprehensive account of the ancient historical circumstances accounting for the lasting and intricate taxonomic confusion surrounding ponderosa and Washoe pines.

Key words: Flora of North America, Pinaceae, Ponderosa complex, *Pinus*, *Pinus washoensis*, *Pinus ponderosa*, taxonomy, taxonomic history, plant conservation, endangered species.

Zusammenfassung

Als Nebenergebnis einer kürzlich abgeschlossenen Studie (LAURIA 1996) wurde *Pinus washoensis* H.MASON & STOCKW. als identisch mit *P. ponderosa* DOUGLAS ex C.LAWSON s.str. (der 'North Plateau Rasse' der *P. ponderosa* var. *ponderosa* in gegenwärtiger Umschreibung) befunden und als deren Synonym zurückgestuft. Dieses Ergebnis widerspricht nicht nur jenem vieler anderer Autoren; die weiter als 'rar' angesehene 'mystische' Washoe Kiefer ist noch immer Gegenstand gezielten Artenschutzes. Es erscheint daher erforderlich, nicht nur alle taxonomischen Beweise für die nunmehr notwendige Relegation der *P. washoensis* als Synonym der *P. ponderosa* herauszustreichen, sondern auch die historisch weit zurückreichenden, komplizierten Umstände zu erläutern, die zu diesem nachhaltigen taxonomischen Wirrwarr zwischen Ponderosa und Washoe Kiefern beigetragen haben.

Introduction

Pinus washoensis H.MASON & STOCKW. (1945) has long been an object of active research, because it is presumed to be of very restricted distribution, in fact one of the rarest pines of western North America. Despite occasional hesitation (e.g. HALLER 1965; HOLMGREN & REVEAL 1966; CRONQUIST & al. 1972; ARMSTRONG 1980; LAURIA 1991), its specific validity was generally not questioned for now more than 40 years (LITTLE 1953, 1979; MIROV 1967; MUNZ 1968; LITTLE & CRITCHFIELD 1969; GRIFFIN & CRITCHFIELD 1972; LANDRY 1974, 1978; MURRAY 1982; FARJON 1984; SILBA 1984, 1986; HICKMAN 1993; KRAL 1993; KARTESZ 1994; for distribution maps see CRITCHFIELD & LITTLE 1966; LITTLE 1971; CRITCHFIELD 1984a). Its inclusion in FARJON (1993) confirms the status of *P. washoensis* as a 'name in current use'.

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Doubts of the present author were first aroused by the realization, based on descriptions of Washoe pine available in the literature, that perhaps more individuals of this species are grown in Austria, in experimental plantations and for ornament, than probably exist among the few accepted Washoe pine populations in northeastern California and adjacent Nevada!

Later, these doubts have further been kindled by various reports scattered in the literature that populations very similar to Washoe pine have also been observed farther to the north, in fact as far north as on Promontory Hill, near Merritt, in British Columbia, in places all well within the range of the 'North Plateau race' of ponderosa pine (HALLER 1965, 1984; see listing in NIEBLING & CONKLE 1990: 307). Despite their implication for the taxonomy of Washoe and ponderosa pines, these reports have all notoriously remained neglected and unverified to the present day. Washoe pine is time and again reported to be rare and/or perhaps even an endangered species deserving special conservation (see e.g. LITTLE 1975; FARJON & al. 1993; but it is beyond the scope of this paper to track down more of these special purpose inventories).

With conservation becoming more and more important in recent times, it is clear that the allegedly rare Washoe pine has received and still is receiving considerable attention from workers in several botanical fields (see next section). Botanical, biochemical, ecological, genetic, and other characteristics of Washoe pine have repeatedly been compared to those of *Pinus ponderosa* s.l. and other taxa. Despite tentative suspicions that hybridization with ponderosa pine (e.g. BILLINGS 1954) and even introgression with it (HALLER 1959a, 1961, 1965, 1984, 1987) may be involved, all other workers have consistently kept the two taxa distinct. RUNDEL & al. (1977) vaguely defined *P. washoensis* as a "high elevation form" of ponderosa pine.

Contrary to all this, *Pinus washoensis* was recently found to be altogether identical (conspecific) with *P. ponderosa* s.str. (presumably corresponding to the North Plateau race of *P. ponderosa* DOUGLAS ex C.LAWSON var. *ponderosa* in its current circumscription). A comparison of the type of Washoe pine and the neotype of ponderosa pine (LAURIA 1996) fully confirmed earlier scepticism. Since this finding differs fundamentally from opinions held by a majority of taxonomists, a summing up of all evidence pertaining to the necessary relegation of *P. washoensis* into synonymy seems appropriate, including an account of the probable sources of the intricate taxonomic confusion surrounding Washoe and ponderosa pines.

The intricately related histories of Washoe and ponderosa pines

The history of *Pinus washoensis* is profoundly influenced by that of ponderosa pine. MASON & STOCKWELL (1945) coined their new species following observations and collections in 1938 and in subsequent years, on the east side of Mount Rose, Washoe County, Nevada. They distinguished Washoe pine mainly on the basis of its "diminutive cones", and differences "in biochemistry, structure and behaviour" (in breeding experiments), it showed in comparison with *P. jeffreyi* BALF., its common forest associate at the type locality, and to which it moreover also resembled in "general aspect". *P. ponderosa* is not mentioned at all in this paper (MASON & STOCKWELL 1945). Two other populations in extreme northeastern California have since also been identified as Washoe pine: In the Warner Mountains (HALLER 1961) and in the Bald Mountain Range (CRITCHFIELD & ALLENBAUGH 1965).

By 1945 a program of study of the species (breeding experiments and chemical analyses specifically mentioned in MASON & STOCKWELL l.c.) had already been conducted for seven years, either with Washoe pine alone, or in combination with other pines. Later, papers documenting results of studies and experiments continued to be issued and testify to the wide interest in the species: MIROV (1948, 1953, 1954, 1957, 1961), HAAGEN-SMIT & al. (1950), and SMITH (1967a, 1967b, 1971) investigated the composition of wood turpentine of many pines and how to interpret it. MILLER (1950) researched the pest resitance of, and DUFFIELD (1953) appropriate pollen collection dates for western pines and their hybrids. RIGHTER & DUFFIELD (1951), and LIDDICOET & RIGHTER (1960), enumerated interspecies hybrids obtained from artificial crosses among western pines, KENG & LITTLE (1961: e.g. table 14) described needle traits, and LITTLE & RIGHTER (1965: 33-35) presented formal botanical descriptions of these pine hybrids. WRIGHT & al. (1969) published early results of a performance study with ponderosa and Washoe pine provenances, JENKINSON (1980) and BURDON & LOW (1991) accounts of their silvicultural experience with these taxa. Among many other pine taxa SAYLOR (1972) also investigated the karyotype of Washoe pine. Results of genetic studies of, and summaries of hybridization experiments carried out including Washoe pine, have been commented by DUFFIELD (1952), CRITCHFIELD (1966, 1984a), CONKLE & CRITCHFIELD (1988), and NIEBLING & CONKLE (1990). Other studies have dealt with the ecology (HALLER 1959a, 1961; SIGG 1987; RIEGEL & al. 1990; WILLIAMS 1996), the phytogeography (HALLER 1965; CRITCHFIELD & ALLENBAUGH 1965, 1969), with the conservation (LITTLE 1975; ARMSTRONG 1980), or the reproductive biology of Washoe pine (MITTON & al. 1996). These studies all revealed that *Pinus washoensis* had more in common with *P. ponderosa*, than it had with Jeffrey pine.

However, *Pinus ponderosa* is a highly variable pine. Taxonomists, though not always with great conviction, normally distinguish two varieties, the type, variety *ponderosa*, and var. *scopulorum* (ENGELMANN 1879). On the basis of differences in some vegetative traits important in forestry, in biochemistry, inherent growth potential and ability to intercross, several geographic races have been recognized among these varieties (reviewed in CONKLE & CRITCHFIELD 1988). The type variety itself has been informally subdivided into two to three poorly characterized geographic races (see distribution maps in CRITCHFIELD 1984a; CONKLE & CRITCHFIELD 1988): The 'North Plateau race' (distributed mainly from northern California to British Columbia), the 'Pacific race' (which occurs throughout most of California), and a third race in southern California, of which very little is known so far. The significance of these racial differences for ponderosa pine taxonomy is still unclear but could be substantial (see further down, and CALLAHAM in prep., pers. comm. 1995), and a comprehensive taxonomic revision of *P. ponderosa* s.l. is indeed desirable (SMITH & al. 1969: 9; KRAL 1993: 391). Studies towards a revision are in progress (CALLAHAM l.c.; LAURIA in prog.) and have so far resulted in the neotypification of *P. ponderosa* (LAURIA 1996).

It is therefore not surprising (as already noted by LAURIA 1996) that workers in different parts of the type variety's range alone, still have quite different notions of some of the main characters of *P. ponderosa* s.str. It must be pointed out that David Douglas discovered and collected *Pinus ponderosa* in the Columbia River region. Many recent floras of western North America (see e.g. SMITH & WHEELER 1992) accordingly state "Spokane River, Washington", as the "type locality" for *P. ponderosa* s.str., an area well within the range of the North Plateau race of modern authors. In order to correctly (neo)typify *P. ponderosa* (LAURIA 1996), this circumstance has of course been taken into account. However, due to historical reasons that have already been detailed elsewhere (LAURIA 1997), it is the Californian ponderosa pine, the Pacific race of modern authors (rather than the North Plateau race of Douglas' general type area), which is since long erroneously, but perseveringly considered by most other authors to represent the botanical 'archetype' of *P. ponderosa* in general. As 'archetype', the Pacific race of California has more than once been extensively studied from the botanical (e.g. SUDWORTH 1908; HALLER 1959b, 1962) and other points of view (reviewed in CONKLE & CRITCHFIELD 1988). Evidence is accumulating from these studies that North Plateau and Pacific ponderosa pines are separate entities (see further down). The recently designated neotype of *P. ponderosa* s.str. (LAURIA 1996) confirms this view.

Contrary to the Pacific race, North Plateau ponderosa pine has mainly remained overlooked for the past c. 150 years and clearly is the one race least studied from the botanical viewpoint. Indeed, despite some data summarized from scattered sources by CRITCHFIELD (1984a: 159-162), no full first hand botanical study of *P. ponderosa* of the northwest, the so called North Plateau race of ponderosa pine at all exists in the literature, including HALLER, whose short abstracts of papers (1965, 1984) testify to his personal surveying of at least some populations of North Plateau ponderosa pine. A renewed and comprehensive botanical survey and documentation of North Plateau ponderosa pine may well bring to light interesting discoveries. In view of the widely held but false notion of a Californian 'archetype' of *Pinus ponderosa* and the inadequate knowledge of the North Plateau race, it is not surprising that the factual status of Washoe pine has remained obscure.

HALLER, for example, recorded additional isolated occurrences of Washoe pine in Oregon and even in British Columbia (Promontory Hill). But, these discoveries only led him to suggest that these populations could have arisen through hybridization between ('typical'!) Pacific, and Rocky Mountain races of *P. ponderosa* (HALLER 1965). Alternatively, he suggested (HALLER 1984) that Californian ponderosa (altitudinal range 100 - 2300 m a.s.l., or no higher than lower montane forest!) could - in California - be prevented by Jeffrey pine to reach borderline subalpine forests (!) at elevations (up to 2750 m a.s.l. [MIROV 1967]) which are in fact reached by North Plateau ponderosa pine farther north, where *P. jeffreyi* is absent. Surprisingly, despite numerous other hints also tentatively indicating this, the possibility that Washoe pine and North Plateau ponderosa pine could be identical was not even cursorily considered; nor has the actual extent of geographical distribution of these northern Washoe pine populations ever been surveyed.

CRITCHFIELD (1984a) intensively studied Washoe pine in the field, although again only in its very restricted known range in northeastern California and adjacent Nevada. He summarized all the botanical data then available on *Pinus washoensis* (p. 158-162), data which he found to clearly link Washoe pine "most closely" to the North Plateau race of *P. ponderosa*. Again, the possibility that these two entities could be identical has not in the least occurred to him. However, CRITCHFIELD also nowhere indicates to have personally studied populations of North Plateau ponderosa pine.

Based on studies by SMITH (1967a, 1971), CRITCHFIELD (1984a) defined Washoe pine turpentine to be characteristically high in 3-carene and low in limonene. These results initially led SMITH (l.c.) to link Washoe pine to Rocky Mountain ponderosa pine (var.

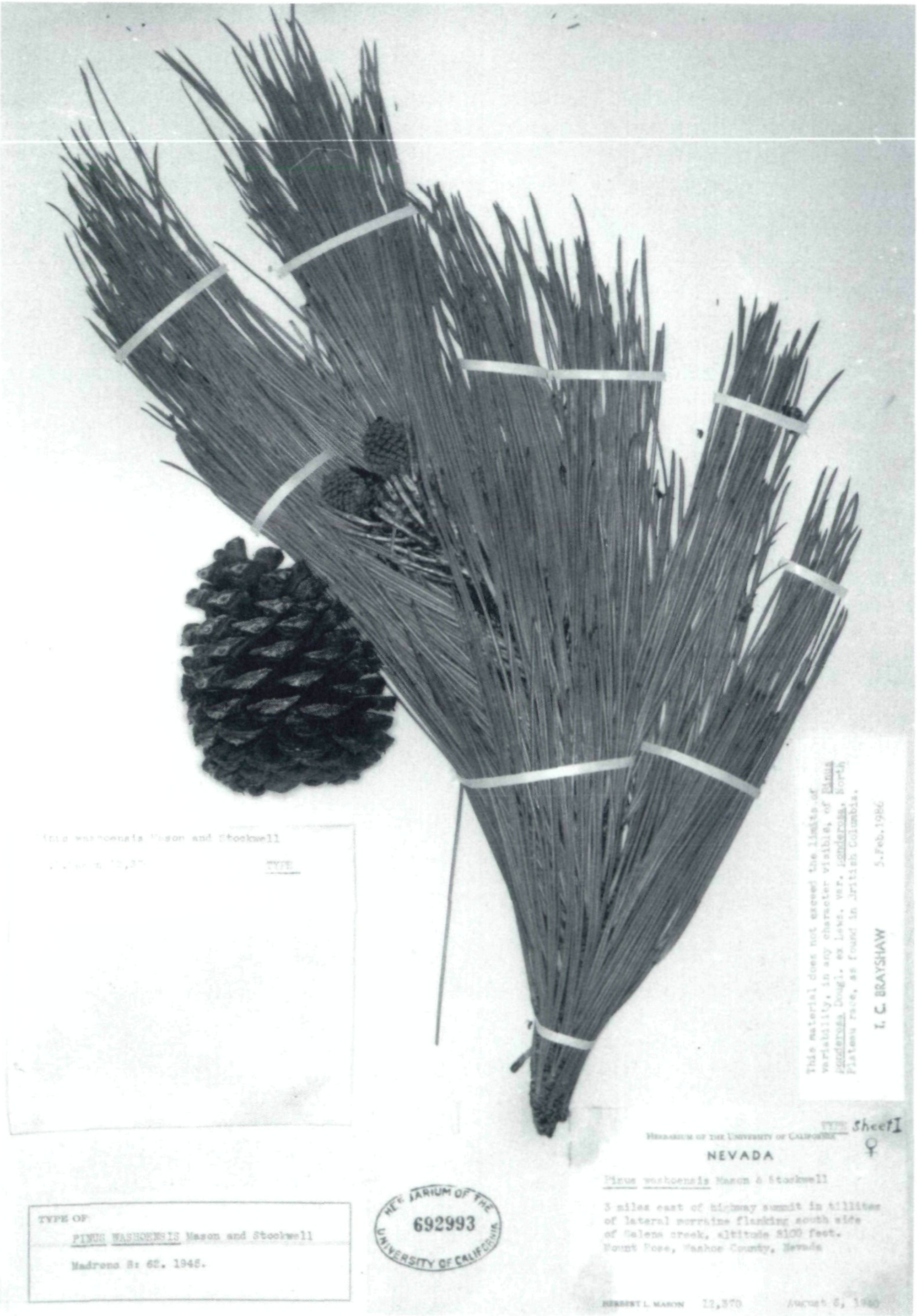

Fig. 1: Lectotype of *Pinus washoensis* H.MASON & STOCKW. [UC], for details see text.

scopulorum), whose turpentine showed to be similar. Later, a range-wide investigation of the monoterpene composition of ponderosa pines also included North Plateau provenances (SMITH 1977). CRITCHFIELD (1984a: 149-150) commented the results of this study as follows: "Throughout the broad distribution of ponderosa pine, only the North Plateau and Rocky Mountain races have frequencies of low-limonene, high-carene trees approaching that of Washoe pine. This combination was most common in 627 North Plateau trees sampled by SMITH. The Rocky Mountain race is more variable".

Many current hypotheses of phylogenetic relationships within and among groups of pines (e.g. among *Ponderosae* and *Australes*) have been formulated on the basis of the crossing behavior of constituent taxa (DUFFIELD 1952; CRITCHFIELD 1963, 1966, 1984a). A cursory check of the relevant literature soon reveals that the data on which these far reaching conclusions of relationships have been based are often incomplete. This particularly applies to ponderosa and Washoe pines. For example, controlled crosses with Washoe pine as one parent have only been attempted with the Pacific, and the Rocky Mountain races (*P. ponderosa* var. *scopulorum*), but very surprisingly never with North Plateau ponderosa pine (CRITCHFIELD 1984a: table 3). All summaries of crossing data (CRITCHFIELD 1984a: table 3; CONKLE & CRITCHFIELD 1988: fig. 7) even clearly indicate that North Plateau ponderosa pines have obviously never been included in crossing trials with other pines of subsections *Ponderosae* and *Australes*, or with pines of any other group. *P. ponderosa* var. *ponderosa* parents used in controlled crosses with other taxa have only been selected from native stands in central California (CRITCHFIELD 1963, 1966, 1984a; CONKLE & CRITCHFIELD 1988), the Pacific race of modern authors.

However, as can be inferred from their differential behavior in controlled mutual crosses (CRITCHFIELD 1984a), it is very probable that ponderosa pine races differ in crossability with other taxa (as also admitted by CONKLE & CRITCHFIELD 1988: 40). Considering this probability, it is very likely that the current hypotheses of interrelationships between *Pinus ponderosa*, *P. washoensis*, and other taxa (CRITCHFIELD 1984a; CONKLE & CRITCHFIELD 1988), and the separation of *Australes* and *Ponderosae* into different subsections (as proposed by DUFFIELD 1952; and upheld by CRITCHFIELD 1963, 1966), are erroneous and misleading, as these inferences are based on fragmentary crossing data. CRITCHFIELD (1984a: 163) fully admitted this but nonetheless avoided the consequences and attached relatively more importance to the results of precisely these incomplete crossing experiments: In view of the seemingly total absence of crossing barriers between Washoe and Rocky Mountain ponderosa pines, he tentatively favored the hypothesis that the former is a geographical offshoot of the latter. Interestingly, in another context, CRITCHFIELD (1984b: 106) took an entirely different view and suggested that Washoe pine is a Pleistocene offshoot of northwestern (the North Plateau race [!] of) ponderosa pine.

The origin and relationships of Washoe pine provided a noteworthy problem also for AXELROD (1986), to whom reports by HALLER (1965) that Washoe pine is scattered discontinuously, from northeastern California through eastern Oregon into interior British Columbia, seemed inconsistent with the assumed relict nature of the species on the eastern slopes of the Sierra Nevada. Based on results obtained by CRITCHFIELD (1984a, absence of reproductive barriers between Washoe and Rocky Mountain ponderosa pines), and based on the personal observation that *Pinus arizonica* ENGELM., and some Cordilleran populations of *P. ponderosa* var. *scopulorum* ENGELM., both produced cones

Fig. 2: Isotype of *Pinus washoensis* H.MASON & STOCKW. [UC], for details see text.

Fig. 3: Cone of *Pinus washoensis* from isotype in [UC]. Size 67 x 68 mm.

very similar to those of *P. washoensis*, he concluded that Washoe pine is an offshoot of some Cordilleran alliance of ponderosa pine. Informative figures of ovuliferous cones of Washoe, Arizona and Rocky Mountain ponderosa pines are provided to exemplify this. As far as this assemblage of taxa is concerned AXELROD was quite correct. If, however, North Plateau provenances would also have been included in the comparisons, AXELROD's conclusions would presumably have been quite different. Washoe and North Plateau ponderosa pines are more similar in many respects than are Washoe pine and

Fig. 4: Cone of *Pinus ponderosa* DOUGLAS ex C.LAWSON, the neotype [W] (LAURIA 1996): Size 88 x 74 mm.

Rocky Mountain races of ponderosa pine. For example, while immature cone colour for both, *P. ponderosa* var. *scopulorum* and *P. arizonica*, is green, this colour is deep purple not only in Washoe pine, but also in *P. ponderosa* s.str. (presumably identical with North Plateau ponderosa pine in general). Washoe pine populations on Mount Rose, Nevada (and on other sites in extreme northeastern California), although now recognized to be North Plateau ponderosa pines, would still have to be called relicts, but of a northwestern element surviving at the very edge of the Great Basin.

NIEBLING & CONKLE (1990) presented the first direct and deliberate comparison of Washoe and North Plateau ponderosa pines. Had the current *Pinus ponderosa* taxonomy been less ambiguous, this study would presumably also have resulted in the relegation of Washoe pine into synonymy, and in a final resolution of the confusion surrounding the two pines. However, this study not only suffered from that 'Californian preconception' alluded to above (of what *P. ponderosa* s.str. is like), and from a persisting misinterpretation of all data clearly indicating a much wider distribution of Washoe pine than currently believed. Contrary to the material of *P. washoensis* used in this study, the provenances of North Plateau ponderosa pine also merely consisted of botanically unverified material on file (determined only according to geographic source), and collected by subsidiary personnel (see the section 'Materials and methods' in NIEBLING & CONKLE 1990). The confusion passed therefore again undetected. The authors did find Washoe and North Plateau ponderosa pines to be similar in botanical characteristics, and only separated by extremely low genetic distance values (considerably less than values delimiting geographic races, see data in next section). However, despite these clear results, NIEBLING & CONKLE (1990: 304, 307) not even tentatively question, neither the specific status of *P. washoensis*, nor its presumed narrow endemism in northeastern California. More recently, this misinterpretation of data was further disseminated by CONKLE (1992), and by STRAUSS & al. (1992).

Summary of evidence for relegating Washoe pine into synonymy

Although MASON & STOCKWELL (1945) provided a quite detailed technical description of their new species (*Pinus washoensis*), they omitted to supplement it with figures revealing its main botanical characteristics. Considering its presumed rarity and, consequently, the restricted familiarity of most taxonomists with this new taxon, only very few figures of (for example) female cones exist in the literature (representative figures are only in: ARMSTRONG 1980; AXELROD 1986; see also: GAUSSEN 1960; FARJON 1984). Although many workers do not routinely consult type material, types are the primary source of information for identification, in particular in this case. The two sheets originally designated as the type of *P. washoensis* H.MASON & STOCKW. [H.L. Mason 12370, UC Nos 692993 and 692994] are shown in Fig. 1 [sheet 1: shoot with ovulate conelets and ripe cone] and Fig. 2 [sheet 2: shoot with staminate conelets and another ovuliferous cone].

For the purpose of clarity and correctness of nomenclatural usage, *H.L. Mason* 12370 (sheet No. 1) [UC 692993] is designated as lectotype (see Art. 8 and 9 of ICBN, GREUTER & al. 1994). The other sheet [UC 692994] represents an isotype, other isotypes are in CAS, DS, NY, US (FARJON 1993, TIEHM 1996). All further specimens cited in the protologue are thus paratypes.

Fig. 3, an enlarged view of an ovuliferous cone of *Pinus washoensis* from sheet 2, is facing Fig. 4, showing the neotype-cone of *P. ponderosa* designated in LAURIA (1996), where some botanical characteristics presumably representative for this species are also given. This account indicates that the ranges of variation in foliage, cone and seed characteristics of *P. ponderosa* s.str. and Washoe pine indeed overlap. Especially seed cones, which are most important for the identification of pines, are very similar in both taxa (purple coloration during maturation, general appearance and shape [small, generally symmetrical, globose-ovoid to ovoid-elongated]).

Attention is directed to corresponding annotations appended to both type sheets enumerated above: "This material does not exceed the limits of variability, in any character visible, of *Pinus ponderosa* DOUGL. ex LAWS. var. *ponderosa*, North Plateau race, as found in British Columbia. T.C. Brayshaw 5.Feb.1986". In a recent publication, BRAYSHAW (1996: 64, 65) confirms his earlier finding by stating: "The Washoe Pine (*Pinus washoensis*) recorded from Promontory Hill, near Merritt [B.C.] ... is a high-altitude form of our northern Ponderosa Pine (var. *ponderosa*) ... There is no discontinuity in altitude or in the range of variation between these pines. In fact, the range of variation in Washoe Pine falls within that of normal Ponderosa Pine. ..."

The combination of constituents of Washoe pine turpentine (SMITH 1967a, 1971) is also most similar to that found in North Plateau ponderosa pines (SMITH 1977). Therefore, CRITCHFIELD (1984a: 163) well concedes that "most evidence (other than crossing behavior) supports the hypothesis that Washoe pine is most closely linked to the North Plateau race of ponderosa pine". CRITCHFIELD (l.c.) moreover also admits that the available crossing data only provide an incomplete picture of crossability among (races of) ponderosa and Washoe pines. The hypothesis of his choice, stating that "in its ability to cross with other taxa, Washoe pine behaves like a fragment of the Rocky Mountain race stranded at the western edge of the Great Basin", thus rests on only fragmentary data.

The study of NIEBLING & CONKLE is replete with data linking Washoe and North Plateau ponderosa pines (see also foregoing section): In all combinations examined, the calculated mean genetic distance values (Washoe - Washoe pines [0.003]; Washoe - North Plateau ponderosa [0.004]; Washoe - Pacific ponderosa [0.013]; North Plateau ponderosa - Pacific ponderosa [0.011]; Washoe - Rocky Mountain ponderosa [0.066]; North Plateau ponderosa - Rocky Mountain ponderosa [0.060]) are quasi identical for Washoe, and North Plateau ponderosa pines (NIEBLING & CONKLE 1990: 304). The authors well admit that "the average genetic distance between Washoe pine and the North Plateau race of ponderosa pine is comparatively small (0.004), and is within the range of distances for comparisons among the three populations of Washoe pine (0.004)" (1990: 304). The authors continue by stating (1990: 307) that (according to NEI's [1974] generalized scale) "species are characterized by distances of from 0.1 to 1.0, subspecies and varieties by 0.02 to 0.2, and races by 0.01 to 0.05", and they admit that "the genetic distance separating Washoe pine from North Plateau ponderosa pine [0.004] was substantially less than the range given for races".

The botanical characteristics of nearly all trees of *Pinus ponderosa* seen by this author in 1992, during a survey of veterans of this species surviving in Great Britain and grown from seeds imported by Douglas in 1826 (LAURIA 1996), well corresponded to the characteristics generally given also for *P. washoensis* (MASON & STOCKWELL 1945; CRITCHFIELD 1984a). The same applies to the great majority of *P. ponderosa* trees planted in Austria, either as ornamentals, or in experimental plantations. All evidence considered, the conclusion is unavoidable: *P. washoensis* H.MASON & STOCKW. and *P. ponderosa* DOUGLAS ex C.LAWSON are identical (LAURIA 1991, 1996; CALLAHAM in prep., pers. commun. 1995).

Other implications and suggestions for further work

Irrespective of the results of taxonomic revisions underway (CALLAHAM in prep., pers. commun. 1995; LAURIA 1991 and in progr.), the results of this review (and LAURIA 1996) have also more immediate implications for the infraspecific taxonomy of *Pinus ponderosa* s.l: If Washoe pine deserved specific distinction when compared to Pacific ponderosa pine, but proves to be only a synonym of *P. ponderosa* s.str (presumably identical with North Plateau ponderosa pine), it would follow that North Plateau and Pacific ponderosa pines in their current circumscription cannot be conspecific. This consequence would also be well supported by other data. Apart from botanical characteristics separating the two 'races', the North Plateau populations, Douglas' *P. ponderosa* s.str., also grow in a somewhat different climate (a summer-rainfall, although low precipitation regime, as opposed to the strict summer-dry conditions prevailing in the area of the Pacific race in California, [CONKLE & CRITCHFIELD 1988]). Attempts at crossing North Plateau and Pacific ponderosa pines (CRITCHFIELD 1984: 151-152, 156, 158), have shown these two races to be partially isolated by reproductive barriers. And, the North Plateau race has probably also experienced an evolutionary history very different from that of the Pacific race (LAURIA 1991). According to immunological comparisons by PRAGER & al. (1976), Washoe pine (vulgo *P. ponderosa* s.str., or North Plateau ponderosa pine) has an antigenic distance value of 0.6 from (the Pacific race of !) ponderosa pine (for origin of material employed see PRAGER & al. 1976: table 1). This already considerable distance value between North Plateau and Pacific races approaches, or is even greater than the antigenic distance value between (Pacific) *P. ponderosa* and more distant taxa such as *P. coulteri* D.DON (0.8), *P. banksiana* LAMB. (0.7), *P. sabiniana* DOUGLAS (0.5), and *P. jeffreyi* BALF. (0.4).

At first sight the comparatively high value of genetic distance between Washoe/North Plateau and Pacific ponderosa pines obtained by PRAGER & al. (0.6) would seem to be at variance with the very low values obtained by NIEBLING & CONKLE (1990: 0.011-0.013, see foregoing section). However, on closer inspection the following circumstances emerge. Like most other researchers working with the Pacific race of *Pinus ponderosa*, PRAGER & al. also collected their ponderosa pine material from natural stands in the vicinity of Placerville in central California, where all the trees of Pacific ponderosa used in all crossing trials also originated from. Sierra Nevada western slope ponderosa pines from this area are thus generally regarded as representing the typical Pacific race of modern authors. NIEBLING & CONKLE, on the other hand, are the only workers who gathered their material of 'Pacific ponderosa' from the near vicinity of Washoe pine stations in extreme northeastern California and in western Nevada. In their section 'Materials and Methods' (1990: 300) they state the following:

"The lower elevation limits of Washoe pine generally coincide with, or exceed, the upper elevational limits of ponderosa pine: the two species contact one another in the Warner Mountains and are separated by 1.5 km distance and 250 m elevation on Mount Rose. ..... [Pacific] ponderosa pine foliage samples for making local comparisons between Washoe and [Pacific] ponderosa pines were collected from neighboring ponderosa pine stands: 65 [Pacific] ponderosa pines were sampled from a stand 10 km west of and 600 m lower elevation than the Washoe pine population in the Warner Mountains and 55 were sampled from a stand 2 km east of and 500 m lower elevation than the population at Mount Rose. The Mount Rose stand of ponderosa pine is typical of the east side phase of the Pacific race, but the Warner Mountains' stand falls within a transition zone between the Pacific and North Plateau races ..... While recognizing that these two stands are insufficient to fully characterize variation in the Pacific race, we list them in this paper as representatives of that race" (additions in [brackets] are from the present author).

With "east side phase of the Pacific race" NIEBLING & CONKLE obviously allude to the ecologically (RUNDEL & al. 1977) and also silvically (MCDONALD 1983) different ponderosa populations on the eastern slopes of the Sierra Nevada (see also HALLER 1959b). And concerning 'Pacific ponderosa' from northeastern California (Warner Moutains), these authors well admit their transitional status (also pointed out by HALLER 1961) between more typical Pacific, and typical North Plateau ponderosa pines. NIEBLING & CONKLE also omitted to document the botanical characteristics of their samples. Considering the confusion that generally exists concerning the various poorly characterized races of *Pinus ponderosa*, and considering the near proximity of Washoe and (transitional) 'Pacific-North Plateau' populations at the sampling sites, including all the other limitations also admitted by these authors, doubts seem justified whether NIEBLING & CONKLE's results also apply to the Pacific race, as meant by all other modern workers.

So, the more studies towards a revision of ponderosa pine and its group progress, the more it becomes clear that further taxonomic conclusions must be postponed until a thorough botanical survey of *P. ponderosa* s.l. has been completed. The credibility of results of future investigations of, and experiments with *P. ponderosa* s.l. may largely depend on the meticulous recording and documentation of the botanical characteristics (good voucher specimens), and the exact source (not only according to seed collection zones or other purely geographical criteria) of the ponderosa pine material employed in these studies.

Apart from this, it has also become evident that the current hypotheses of relationships of *Pinus ponderosa* are very questionable, simply for the fact that they are based on only fragmentary crossing data. Since ponderosa pine 'races' differ in crossing behavior with other pine taxa (CRITCHFIELD 1984a; CONKLE & CRITCHFIELD 1988), an investigation of the still unknown behavior of *P. ponderosa* s.str. (presumably corresponding to North Plateau ponderosa pine) in crossing trials with other taxa of subsection *Ponderosae* (and *Australes*), would seem to be the most urgent future work to be recommended.

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Note added in proof

By the time the present author had quite incidentally noticed a review (W. J. Appl. Forest. 12: 4, 1997) of Dr. T.C. BRAYSHAW's recent book (1996), including the specification that this author had also addressed the subject of Washoe pine and its relationship to ponderosa pine, the present paper had already been submitted for publication. Following the timely receipt of a copy of his book, revising the present manuscript after the peer review process provided an opportunity to incorporate at least a short reference to Dr. BRAYSHAW's account and conclusions (see above), which proved to be quite similar to those arrived at in this paper. Correspondence subsequently initiated in view of this coincidence brought to light that Dr. BRAYSHAW had obtained his mainly still unpublished results already more than 10 years ago, and based on experiment, morphometric comparisons and detailed observations in situ. Considering the interesting fact that his study and the present review largely complement each other, and although the deadline for submissions had long passed, every possible effort was made, and I wish to express my sincere thanks to the members of the editorial board for their obliging cooperation, to accommodate both papers in the same forthcoming issue of these 'Annals' (see also this volume, pages 673 - 680).