Some problems concerning the conception of species especially within dendrology

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Not only dendrology but the biological science as a whole is conserned with – or to a certain degree stimulated by – what may be called the species-problems. These are mainly the following. I. Taxonomical misunderstandings, e.g. *Populus deltoides* Marsh., which was supposed to be common as a tree in Denmark, until it grew clear, that we do not have it at all. It had been confused with *Populus* \times *canadensis* Moench, the hybrid-complex of *P. deltoides* \times *nigra*. II. Misunderstandings due to wrong names in the nurseries and of the imported seeds; f. i. *Hydrangea petiolaris* Sieb. & Zucc. which is nearly always sold if *Schizophragma hydrangeoides* Sieb. & Zucc. is required just as *Tsuga diversifolia* (Maxim.) Mast. in stead of *T. Sieboldii* Carr.

III. Misinterpreting from hybrids. In the Botanical Gardens and Arboretums very often a single specimen of a certain species is surrounded by some more or less closely allied species and thus, correctly named itself, may produce any amount of hybrid seed perhaps mixed with its genuine offspring, but all of it delivered as seeds from the species in question. Especially when the species is selfsterile or has a pronounced dichogamy hybrids may be the result. Likewise in plantations f.i. of Abies Nordmanniana (Steven) Spach in the vicinity of A. alba Mill. or Picea sitchensis (Bong.) Carr. growing close to P. glauca (Moench) Voss the dichogamy may cause lots of hybrids in the offspring. Mostly these hybrids will show a pronounced heterosis and as the most fast growing plants are liable to be selected by man, these will cause a wrong idea of the species among foresters, horticulturists and botanists too. Here may be mentioned Alnus subcordata C. A. Mey. growing extremly well in the Botanical Gardens of The University of Copenhagen, The Royal Veterinary and Agricultural College of Copenhagen, Berlin, Kew and so on. All these trees were considered to be typical and originated from genuine, now dead trees in the gardens from the first import. Of this – as far as I know – only one specimen had survived in Charlottenlund Forestbotanical Garden and here gave SYRACH LARSEN and collaborators the possibility finding out that this species only gave few and weak seedlings by it self but lots of fastgrowing hybrids (triploids) after pollination that nearly always took place from A. *incana* (L.) Moench and A. glutinosa (L.) Gaertn.

Although the above mentioned three points have caused severe species-problems they shall not be mentioned further here. Future investigations may unveil lots of errors in our conceptions, but the now used means of propagations viz. cuttings, scions and controlled pollination will eliminate this source of mistakes.

IV. As another species-problem that has caused some confusion we have the extremely bad custom to use a species name for hybrids and a variety (or even species) name to a mere clone. By this we get quite a false impression of the taxon a species. Salix \times rubra Huds. (S. purpurea \times viminalis) and S. Smithiana Willd. (S. caprea \times viminalis) may be mentioned as such hybrid clones. Populus \times italica Muenchh. (P. nigra italica) may examplify a not hybrid clone. If the hybrid is polymorphic, with several distinguishable types there can be some reason to use a specific name for this unity (e.g. Populus \times canadensis Moench and Ulmus \times hollandica Mill.) Also these cases are of minor importance and the new international rules of nomenclature have prescribed how to use names for hybrids and clones.

The following points on the other hand are very difficult to deal with and the remarks below must be considered to be an attempt to discuss them in order to find a solution although it seems to be impossible with our knowledge of to day.

V. The conflict in view on the delimitation of the species. As we cannot produce a clear definition of the taxon species because the old Linnean based upon creation by God of all living have lost any sense in the light of evolution.

Very often a hybrid between two species will be sterile or at least of a very poor fertility and thus demonstrating that the two parent species really are well defined. This intersterility is often considered to be the true mean of delimitating two species but it must not be forgotten that a species having a large area and perhaps several varieties, let us call them a, b, c, d, e and f from boundary to boundary, may show full interfertility within the following groups, a, b, c, and b, c, d, e, and e, f, while a and d only are partly interfertile and a and f quite intersterile. The question is, do a and f belong to the same species? I should like to answer yes, because they are connected by a series of intergrades but in some thousands of years they may be established as veritable and well defined species.

Not seldom do we find morphologically as well as ecologically clearly distinct species that will produce hybrids of high fertility. So do f.i. several species of *Salix*, *Larix* and – to mention some herbacious plants too – *Geum rivale* L. and *G. urbanum* L. We sometimes find the *Geum*-hybrid in nature but mostly it will disappear in the course of a few years and distinguishable intermediate backcrosses are very, very seldom met with; the two species seem to the only important in nature presumably because of either selection due to competition, or a cytological tendency to reestablish the genoms of the parental species, or the want of suitable growing places for the hybrid. Among trees and shrubs f.i. *Salix caprea* L. and *S. cinerea* L. hybrids and backcrosses seem to be more common; this is probably partly due to their longevity and partly to their dioecious nature. Everybody having studied this complex in nature will know that by far the greater part easily may be referred either to *S. caprea* or to *S. cinerea*.

Thus we may conclude, that in cases of intersterility we mostly have well defined species, and that interfertile species are to be considered as true species if they are clearly preferred as competitors on certain growing places in nature. Often, but not at all always this is a very useful way to distinguish true species but a thorough knowledge to the growing places of the forms in question is inevitable because in the herbariums the number of hybrids and intermediate forms will give quite a false concept of their importance in nature because of a tendency to collect specimens deviating from the main part of the bunch. If intergrades are frequent and of real importance in nature it must be an omen to consider whether it would not be better to amalgamate the two (or more) species into one.

VI. Ignorance concerning the natural variation of a species due to the – from a biological point of view – misleading use of a typespecimen that may be a rare variety of a species or a cultigen type (f.i. in *Aucuba japonica* Thunb. and *Cupressus sempervirens* L. the types are a variegated and a fastigiate form respectively). This point is especially of importance to dendrology because – even when the type-specimen is a representative for the main part of the species – only one or at most a few are cultivated in a garden or an arboretum and either propagated by seeds, producing lots of hybrids, or vegetatively illustrating the invariability not of the species but of the type-

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specimen, the description of which will get a supply of characters added to the original one from observations on the various growing places of this single individuum. We must never forget that there is an enormous abyss between our concept of a new species (a Rock number f.i.) and of an in our mind good old one as f.i. Picea Abies (L.) Karst. Let us suppose that travellers from another part of the world had brought home some seeds of Picea from various parts of the unknown Europe, and that of each collector-number one single specimens grew until fructification in the arboretum, we might have had several well described (but not well defined) species of Picea growing in Central Europe. It is just this that has happened, in many of the Rock collections. From each number one tree is desribed, and this tree is not identical to those representing the same Rock number in other arboretums or botanical gardens. Moreover some of these may be identical to or at least closely allied to the casual type specimens of an other Rock number. It must be admitted that in such cases the type-specimen method makes species problems of nearly an insolvable kind.

In the following we will look upon some trees from western North-America, first two species with rather well defined varieties, then three groups of clearly different species as far as the types are concerned, but in nature connected by intermediate forms which since long have been well known and have raised some confusion, finally an example of four species which are not so distinct as it has been until recently supposed.

1. Pseudotsuga taxifolia (Lamb.) Britt. (which now is said to have to alter its name to P. Menziesii (Mirbel) Franco) is commonly known to have three varieties, viz. P. t. viridis, P. t. caesia and P. t. glauca.

Var. viridis has rather long, green on the upper side somewhat shining needles on the very shallow pulvini. On the branchlets especially on the somewhat shaded, the needles are directed out to the two sides, making the shoots nearly flat. The winterbuds are rather slender, shining and without resin. The resin of the needles and of the barkblisters has a sweet, perfume-like odour. The cones are rather large and only produced in abundance with intervals of 4–5 years. Here in Denmark often badly damaged by *Phaeocryptopus Gäumanni* and *Adelges (Chermes) Cooleyi* but resistent to *Rhabdocline pseudotsugae*. It seems to be confined to cool, moist climates and the best sites.

Var. *caesia* has mostly somewhat shorter needles on larger pulvini. The neadles are more stiff than those of viridis and more or less pruinose bluish colour. The parting of the needles is very imperfect especially on the upper side of the branchlets. The winterbuds are not

so slender as in the former variety and their surface is dull and often covered with scales of dried up resin. The resin has besides more or less of the perfume-odour a pronounced sharp touch of terpeneodour. The cones vary in size and show a more regular production with intervals of a few years. Phaeocryptopus and the Chermes may be common but do not seem to be so grave for it perhaps due to more pronounced frostresistance in caesia. Nor is Rhabdocline of any importance. It is found from the coast to the most dry interior growingplaces for Pseudotsuga; in southern Oregon the viridis has quite disappeared even near the shores of the Pacific thus giving place to pure stands of *caesia* types. Just the same could be seen in the dry interior zone of British Columbia, where caesia was dominant all over, and often nearly blue with characters very close to those of the following variety. Every time mountains brought about moister conditions and spots of better sites viridis types occured in considerable number. This may also be the case in the fog-zone in southern Oregon and North California but I do not know anything about it, I have not been there myself and the Americans do not distinguish between caesia and glauca.

Var. glauca has rather short and stiff needles on very distinct pulvini. The needles are very bluish and often with a shallow emargination at the apex. They are completely without any parting on the twigs. Winterbuds not so dark and not so resinous as in *caesia*. The resin has a pure and rather sharp smell of terpentine. The cones are small with extraordinary long bracts and produced abundantly nearly every year. I have no information about *Phaeocryptopus* and *Adelges* of this but the little I have seen (most glaucas die young here in Denmark on account of severe attacks of *Rhabdocline*) have left an impression that they are of no importance to it. *Glauca* is confined to Colorado where it represents the southeastern outposts of the Douglas-Fir.

We cannot divide *Pseudotsuga Menziesii* into three species, they are all too closely allied. As far as I know they are quite interfertile and not too sharply parted into ecological units, but the occurence and characters of the blue Douglas may allow us to call it an ecospecies.

2. Pinus contorta Loud. and Pinus contorta latifolia S. Wats. (P. Murrayana Balf.) have always been problematic for the Danish foresters and so they are to the Americans too, foresters as well as botanists. After having looked at them myself I find it very illustrating to compare them to Common Mountain Pine (P. Mugo ro-tundata) and Pyrenean Mountain Pine (P. Mugo rostrata).

Pinus contorta, Shore Pine or Shrub Pine is a little tree with broad limbs and dark needles; the bark soon gets thick and scaly, the cones are a little oblique with rather thin conescales and shields. Only very few specimens are closepines. It is found in the coastal zone from Alaska to California growing on poor and dry soil often shrubby but sometimes a rather nice shape. Here in Denmark it is much affected by damage from Tortrix buoliana.

Pinus c. latifolia, Lodgepole Pine, Murravana Pine, is a slender tree with small and fine limbs. The bark remains for a long time rather smooth, with a very characteristic surface due to the resinblisters giving in the aspect of that of a Cherry-tree with lenticels. When the bark finally gets crustaceous it is much thinner than the bark of the first variety which although it has got the species-name without any suffixes is the less important type compared with latifolia which covers large areas. The cones are very oblique and the conescales on the outer side of the cone are thick, with a very thick shield often characterized by a protruded and reflexed umbo. A rather large number of the trees in a stand are closepines, the cones remaining closed for years and the seeds not spread until the cones open after a forest-fire. It grows inland from the Cascades to the Rockies forming large, very dense pure stands presumably owing their existence to forest-fires. These stands are found on rather good soil but on extreme localities: near timberline, on bogs or on sandy fields in the drv interior types reminding in shape and sometimes in a few characters too of the Shore Pine. It must be added that on the westfall of the Cascades quite intermediate forms were met with. Here in Denmark it often thrives rather well and is never affected by the Tortrix. The Americans do not venture to distinguish these two forms as species and call them as a whole Lodgepole Pine or even Jack Pine, which is the name for P. Banksiana. But I must admit, that I find them better distinguished than the types of the Douglas fir at least the viridis and the caesia types.

3. Pinus ponderosa Laws. and P. Jeffreyi A. Murr. represents two well defined species, which differ in several characters and partly in distribution but where they meet they are said to be so mixed in characters, that it is impossible to check them out in the stands. I regret, that I have not seen this transition-zone and have only got a personal impression of ponderosa in the northern part of its area. Pinus ponderosa, has bark reminding of that of a P. nigra but the furrows are of a bright orange red to orange yellow colour. The needles vary in length, but are mostly more than 20 cm long, in colour they vary from greyish green to dark green. The one year shoots are not pruinose and the winterbuds are mostly resinous. Finally the cones are about 10 cm long, remaining for some years on the tree and leaving the lower cone scales on the branch when they fall off. It grows from British Columbia (The dry interior zone) to Colorado and California where it meets the following.

Pinus Jeffreui differs chiefly in the often longer needles, the not orange-coloured bark, the pruinose surface of the one year shoots. the want of resin on the buds and the at least 20 cm long cone which generaly will fall off in the autumn after their opening. American botanists and foresters state that there exist lots of intergrades. Although I have not seen intermediate types of cones, they may exist. but I think that they are rare. I have a suspicion that we here have two well defined and well separated species, and all that has been said about their being two types of one species originate from descriptions of single trees. I have seen in British Columbia and Washington lots of fine specimens of P. ponderosa without resin on the budscales contrary to the original description. And here in Denmark I have met some other typical trees of P. Jeffreyi without pruinose twigs and others with resin on the buds, this is not at all in accordance with the original description. Further investigations may solve this problem.

4. It was mentioned long ago that Abies grandis Lindl. and A. concolor (Gord.) Engelm. were closely allied and connected by A. Lowiana A. Murr. American foresters have been well aware of this and say that they are not able exactly to check the limits between grandis and what they call concolor, which partly must correspond to our true concolor. I have not seen but grandis in America; once in the lower Cascades in southern Oregon they showed me some trees, that they had been told were concolor but admitted, were very difficult to distinguish from grandis. I was quite unable to call them anything but *grandis* although some features in the bark reminded of Lowiana. I regret very much, that I had not time enough to study this problem over there, but I feel sure that this uncertaianty as to determine these types exactly must originate from the total want of any sharp limit between the types. Maps of the area of Abies grandis give this species a rather large area in the lower Rockies in southern British Columbia and northern Washington. I will be really astonished if genuine grandis grows there. The statement must either be wrong or be due to the ocurrence of Lowiana-types. In this connection it must be mentioned that SYRACH LARSEN has pollinated Lowiana with grandis-pollen and got an offspring of several trees, having hardly any characters from the mother-tree.

A. grandis is a coast-bound, lowland-tree with strictly dorsiventral, emarginate needles having shining and throughout furrowy upper surface. The twigs have a very flat parting on both sides, and the bark remains thin with large blisters.

A. concolor is a mountaineous inland-type with isolateral, blunt, not emarginate needles with a dull, not at all furrowy upper surface. On the upper side of the twigs there is not any parting whatsoever. The bark is somewhat like that of *grandis*.

A. Lowiana in the characters of the twigs and needles is quite intermediate between the two former, but the bark is more rough and with less pronounced resin-blisters when young. What has been said represents the common European type of *Lowiana*, but studies in the variation within *concolor*-types make it clear that intermediate forms can be found among them, and I hope and believe that future will disclose a series of intermediates between *grandis* and *Lowiana* growing in the natural forests of America.

In spite of this supposed gradation between the three species I would prefer to consider them as true species because they, as far as I can see, have – each of them – well defined areas of distribution.

5. Tsuga heterophylla (Raf.) Sarg. and T. Mertensiana (Bong.) Carr. are - apart from mistakes arising from their intricate nomenclatural history - even more distinct than the Abies-species, just mentioned. The latter represents such a queer type within *Tsuga*, that a French scientist seriously has suspected it to be of intergenetic hybrid origin (Tsuga heterophylla \times Picea sitchen-sis); but what is of interest to us is that Tsuga Jeffreyi (Henry) Henry is considered to be a hybrid between the Western and the Mountain Hemlock. It has been known from a few localities and was said to grow among the parents. T. heterophylla is easily recognised by its small, always dorsiventral, lanceovate needles, with a very indistinct and irregular serration (at least on grownup specimens; young trees have a much more distinct and somewhat spiny serration. The cones are small and egg-shaped. The leading top-shoot is overhanging in the main part of its first year, and young trees prefer shade, avoiding too dry air and seems to be climax-trees on most forest-soils within the area of the Douglasfir, at least where the green and the not too grey types of Fir thrives well. It is found from the shore to high up in the mountains on their westward slopes reaching some hundred m below timberline.

T. Mertensiana is a tall mountain tree, growing near to timberline

mostly spread among other trees seldom forming pure stands. Its needles are linear, often a little curved, dark green to bluish green, isolateral with lots of stomata on both sides and quite devoid of serration. The cones are large for a Hemlock, in size and shape reminding of those of *Picea glauca*. I have got the impression that it is a light-loving pioneer tree, but rather slow growing. The top-shoot is not or only slightly overhanging.

T. Jeffreyi is, as far as I have seen, met with wherever the two former Tsuga-species grow near each other. The type has quite intermediate needles, these being slightly serrate, broad linear, with a considerable number of stomata on the upper side, but to a certain degree dorsiventral. The cones are nearly half the size of those of Mertensiana, but have the same Picea-like shape. In the Canadian forest literature it is mentioned that intergrades between Mountain and Western Hemlock some times may be found in high altitudes, and I found whenever I climbed to the transition zone between the two main species that a long series of intermediates as to structure of leaves and shape of the trees easily could be demonstrated there. Concerning the cones they seemed to be either heterophylla cones or cones of Mertensiana-shape varying in size from that of Jeffreyi cone to that of a true Mertensiana cone.

I am of the opinion that T. Jeffreyi is a hybrid F1's and backcrosses both of the parents. As a longliving tree and as a pioneer it is more often met with than usually is the case in hybrids, and I should like to call it a woody parallel to the above mentioned *Geum*hybrid and like it being of full or nearly full fertility.

6. Picea glauca (Moench) Voss, Picea Engelmanni (Parry) Engelm. and Picea sitchensis (Bong.) Carr. are three important and apparently easily distinguishable American trees. Here in Denmark we are accustomed to find the hybrid between White Spruce and the Sitka spruce whenever seeds are gathered on Sitkas not too far from White Spruces. In their homeland they only reach each other in some places in Alaska, and I was told that hybrids occurred, but I did not go there. As to P. glauca and P. Engelmanni I was greatly astonished when Canadian foresters told me that it was quite impossible to distinguish between these two species, I really did not believe it. Fortunately I got a chance to study the two trees on several growing places in the Canadian Cascades and in The Gold Range and in the Selkirk Mountains. The P. glauca growing there is the very characteristic variety Albertiana having bark, needles and cones like those of the common eastern White Spruce but distinguished by hairy branchlets and being a slender and tall tree, reaching 50 m and a little more, thus at a distance having just the same appearance as *P. Engelmanni*. Like this it grows on the high mountains but only on dry, often somewhat poor soil, while *Engelmanni* in typical specimens stood on rich wet soil along the streams and the drainage from the snowpatches and between these two types of growing places there was no end at all in the variation of the intermediate forms only arranged in such a way, that the nearer we got to the wet growing places the more dominating grew the *Engelmanni*-characters and vice versa. Thus we may conclude that *Picea glauca* and *P. Engelmanni* are two ends of the same complex connected by *P. Albertiana*, and I find it reasonable to give them all the range of true species. I feel convinced that all sorts of intergrades between *P. Albertiana* and *P. glauca* may be found in Alberta and eastwards.

Picea sitchensis and P. Engelmanni never share growing place, the former being a lowland tree only climbing (along the streams) to a few hundred m, while the second never descends below 1000 m above sea level. Between these two altitudes single spruce trees may be found showing clearly intermediate characters in cones, needles and bark. I have seen such in the Mount Rainier National Park and near The Wind River Experiment Station where mr. LEO ISAAC told me, that there were some curious types of P. Engelmanni far below its normal ocurrence. I have not been able to solve whether these few trees have to be considered as hybrids or true intermediates growing in intermediate altitude; I did not see seeds in the old empty cones nor any seedlings below the old trees. Further investigations are needed.

Finally I want to postulate that intermediate forms also must exist between *P. Engelmanni* and *P. pungens*. We have had such an intermediate tree in Charlottenlund Forest Botanical Garden, but it may of course be the result of seed collection in an arboretum.

Thus I think that we have to deal with 5 distinct but closely allied species belonging to two different of the taxonomists sections: *Eupicea* and *Cassicta*. The five species may be arranged as follows.

P. sitchensis — P. Albertiana \gtrsim P. glauca $\downarrow \uparrow$ P. Engelmanni \uparrow P. pungens

Many other similar cases may be found among other taxonomical units all over the world.