Engler, A. 1881. Ueber die morphologischen Verhältnisse und die geographische Verbreitung der Gattung *Rhus*, sowie der mit ihr verwandten, lebenden und ausgestorbenen *Anacardiaceae*. Bot.Jahrb.Syst. 1: 365 – 426, plate IV.

An excellent example of Engler's earlier style of phylogenetic explanation, which seems to rely more on Haeckel's monophyletic viewpoint than Nägeli's polyphyletic concept, is given in a passage from his study of Anacardiaceae systematics and evolution which accompanies and explains a remarkable dendrogram, itself seemingly a forerunner of W.H. Wagner's (Wagner 1980) groundplan divergence dendrograms (Engler 1881: 398 – 401, plate IV).

[Translation by Simon Mayo, 25 June 2011]

"The main difficulty of phylogenetic investigations lies in the determination of the Primary and the Secondary; it is especially difficult to decide whether a Type which is close to another in a certain respect, is more advanced or more reduced. Formerly one was inclined generally to see the monochlamydeous forms as reduced Types, but now one considers, on good grounds, the reverse. Even less are the Apetalae to be regarded as having arisen by reduction, and it is often difficult to decide whether a plant is a member of the Monochlamydae or of the Apetalae. We have to make this decision in respect of *Haplorhus* and *Pistacia*. It is similar with regard to the androecium. Is an androecium formed of two whorls primary or secondary? We can just as easily surmise the beginning of reduction as of interposition in the fact that in androecia formed of two whorls the stamens of the second whorl are often weaker than those of the first. I havae already indicated earlier that I consider the latter more probable in the Anacardiaceae. But with these theoretical considerations alone, however, one cannot progress very far. Only if all available forms have been studied and especially the development of the vegetative organs considered, can one venture to propose a natural grouping of the genera. The anatomical differences which were established earlier seem to me not really suitable for a division of the Rhoideae; if we were to divide them into two groups according to the presence or absence of resin

canals in the pith, then *Metopium* would be placed in a different group from *Rhus*. And furthermore, various species of *Rhus* differ in this respect.

However, the patterns of geographical distribution furnish important supporting evidence, although a biased consideration of these facts can also lead to error. At any rate, it is always more probable that a genus is linked to others that occur together with it; this consideration will be especially justifiable in genera of tropical regions in which major changes and displacements in plant distribution have happened to a lesser degree. Based on this viewpoint I believe that the evolutionary connections [verwandtschaftlichen Beziehungen] of the Rhoideae can now be represented graphically in the following way.

In the accompanying figure (Plate IV) the branches of the evolutionary tree [Stammbaumes] end at the circumferences of eight concentric circles and what is thus indicated is the stage which each individual genus has reached.

I. indicates an evolutionary stage [Entwicklungsstufe] of T A G {Tepals, Androecium, Gynoecium}, i.e. the flowers are monochlamydeous.

II. corresponds to the the stage C P A G {Calyx, Petals, …}, i.e. the flowers are diplochlamydeous and the androecium is composeed of a single whorl.

III. corresponds to the stage C P A + A G, i.e. there are two stamen whorls present.

IV. corresponds to the stage C P A + A̲ G, i.e. the second stamen whorl is in the process of atrophy or is completely aborted.

Apart from these numbered circles there are four others, denoted with *b*. are by The circles denoted by *a* specify those genera in which the gynoecium has 3 or 2 locules containing ovules, whereas genera in which the gynoecium contains only one ovule are found on the circles denoted by *b*.

The geographical region of distribution is also appended to the name of the genus.

One can see first of all that I have not attached *Thyrsodium* to one of the two major stems to which most of the other genera belong.

The genus *Thyrsodium* is rather isolated by the cup-shaped cavity of the floral axis; it comes closer to the genera related to *Sorindeia* than to those more closely linked to *Rhus*. The rather few differences between *Trichoscypha*, *Euroschinus* and *Sorindeia* have been discussed earlier. The fruits of *Microstemon* and *Parishia* are similar to those of *Sorindeia*, *Trichoscypha* and *Euroschinus*,

especially to those of *Trichoscypha*; the strong enlargement of the calyx segments in the fruit of *Parishia* is indeed a remarkable character, but secondary for the grouping. Apart from in *Pentaspadon* the ovule in all genera of this branch is inserted at the upper end of the ovary locule.

The number of genera which belong to the second major stem is much larger. First we see a small branch separating with *Haplorhus* and *Pistacia*, whose fruits (apart from *Pistacia vera*) are similar to those of *Rhus, Botryceras, Cotinus*; it is however extremely unlikely that *Haplorhus* and *Pistacia* have been the origin [Ausgangspunkt] of any of these genera since they had already attained dioecy. The genus *Protorhus* is the one which has most kept the original Type, if {one imagines that} later only one ovule becomes a seed; also by the simple, undivided leaves it shows itself to be a member of an older Type whose near connections to *Anaphrenium* have already been discussed above. Like the latter genus, *Campnosperma*, particularly different from the other two because of its diplostemony, must also be linked to *Protorhus*. The geographical distribution of this genus in Madagascar, in the Seychelles, in the East Indies, if we take account of *Drepanospermum*, in tropical America, shows also that this genus must be very old. With the Type of *Protorhus* are linked the Semecarpeae, which also have simple leaves, but which have not attained diplostemony. Since the Semecarpeae form such a natural group, I feel their separation as a tribe is justified, but I am quite convinced that they are derived [ihren Ausgangspunkt hatte] from *Protorhus* and *Campnosperma*. The mediterranean genus *Cotinus* agrees with the Cape genera *Botryceras*, *Smodingium* and *Loxostylis* in the lateral position of the style, although closer connections between these genera have not been found; one can only presume that they have diverged from a Type whose origin coincided with that of *Protorhus*. The genera of the closely related group connected with *Rhus* belong to such a Type which however followed a different evolutionary development [andere Entwicklung]. At the same stage as *Rhus* are *Metopium, Comocladia, Pseudosmodingium, Lozopterygium, Schinopsis* and also *Faguetia.*

These genera diverge from *Rhus* first by the nature of their fruits, *Faguetia* additionally by tetramery, *Comocladia* by tetramery or trimery of the flowers. After that the insertion of the ovule in the other genera is different than in *Rhus* and *Metopium*; in the latter it is basal, and in the others inserted at the upper end of the locule, although in *Rhus* sometimes the funicle arises from the side wall and not from the base. All these genera are isostemonous and *Schinus, Lithraea* and *Rhodosphaera* are diplostemonous. The fruits of these three genera are very similar to those of *Rhus* particularly those of *Schinus* and *Lithraea*. The position of the ovule is the same in *Rhodosphaera* and *Lithraea* as in *Rhus*

and in *Schinus* it is inserted at the upper end of the locule. The geographical range of these three genera lies in the southern hemisphere. The range of *Schinus* borders on that of *Rhus* in the Andes; however the single South American *Rhus*, *Rh. juglandifolia*, does not exactly correspond to a Type which could be derived from *Schinus* and *Lithraea*. The fact that in both the leaves are simple and that *Lithraea* is also represented in Australia signifies that their origin is to be sought nearer to *Protorhus* and in the southern hemisphere." (Engler 1881: 398 – 401, plate IV).