Engler, A. 1876. Vergleichende Untersuchungen über die morphologischen Verhältnisse der Araceae. I. Theil. Natürliches System der Araceae. Nova Acta der Ksl. Leop.-Carol.-Deutschen Akademie der Naturforscher 39 (3): 133 – 155.

Translation by Simon Mayo, 25 March 2010.

[Engler here is 32 years old]

Foreword

In recent times one repeatedly perceives that many characters to which a certain morphological and hence also systematic value had been earlier attributed, cannot be considered such, but have rather mechanical causes and are connected in a more-or-less recognizable fashion with the environment of the plant. The evaluation of characters as systematically essential or inessential is well known to be so difficult that in this field there is ample room for the subjective opinion of an individual researcher. Experienced taxonomists well know that general rules on this question cannot be set up and that characters which in one family or one large plant group are of high systematic value, in another have only lesser importance. The only correct way known to proceed in this regard has been to group the different elements [die Formen] of a group of related taxa [eines Verwandtschaftskreises] according to their greater or lesser similarity and then use the results to reach a conclusion on the systematic value of individual characters. It is an even more deep-rooted axiom that the floral parts alone have systematic importance and that the nature of the leaves, leaf arrangement and shoot architecture as well as the anatomical structure of individual organs are of a much lesser degree of importance. It may be true in certain groups of the Dialypetalae or the Monocotyledons, where due to the great number of extant forms the limits of variation of the family-defining characters are drawn more narrowly, and in such cases a unilateral investigation is justified of the leaf and fruit parts and of floral development. The only salvation is often seen to be in ontogenetic development [Entwicklungsgeschichte], and certainly this gives us, when comparative and supported by knowledge of the range of forms [taxa?] often the only clarification of the descent relationships [verwandtschaftlichen Beziehungen], whose discovery is always the goal of systematic investigations that are otherwise very dull and of little practical application, whether one brings into the concept of relatonship [Verwandtschaft] the idea of heredity or starts out from definite prototypes capable of transformation up to a certain level. In the appreciation of the floral organs for systematics, however, the anatomical nature of the vegetative organs is all too often neglected. The reason for this lies in the fact that relatively few botanists who possess a sufficient knowledge of the range of species are also experienced in morphological-anatomical investigations. Even more rarely is shoot organization considered, because younger botanists find only little about it even in the best botanical handbooks [textbooks] and also receive little direction for such investigations in most botanical courses [Vorlesungen]. On these grounds, some groupings, in families where investigation of floral organs is very complete, are still to be regarded as unnatural. This is the case in the family Araceae, for which the earlier, highly merited monograph of Schott, by means of its very careful and exact investigations of floral structure, first provided the basis for a scientific knowledge of a group of equal interest to both botanists and gardeners. As I undertook the treatment of the Araceae

for the Flora Brasiliensis and also took up the task of working up the whole family as a systematic monograph for the Monograph series of De Candolle, I soon recognized how urgently needed it was to repeat the kind of morphological investigations made by Al. Braun and Irmisch on some Araceae, using all material available to me. It was also just as necessary to carry out comparative anatomical investigations. Scattered data [on this subject] exist, but unfortunately these are defective because the authors relied on incorrect determinations [of their specimens] which are often widespread in cultivated collections [in den Gärten], and so the most contradictory results would appear if the data from the various authors were referred to the plants which had been [thus] named. It should be noted here that anatomical characters should only be applied to classification with great care, since many comparative anatomical studies have shown that the same or similar anatomical conditions occur in plant groups which systematically certainly do not belong together and could absolutely not be connected by relationship [welche systematisch zweifellos nicht zusammen gehören und durchaus nicht in verwandtschaftlicher Beziehung stehen können]. This is particularly relevant to the distribution of the fibrovascular and phloem strands. In fact the earlier comparative anatomical studies carried out by van Tieghem on the Araceae have shown that the groups of Araceae based on the distribution of fibrovascular bundles do not correlate with the groups of Schott's system of the Araceae and that genera of the most profound natural relationship [natürlichen Verwandschaft] belong to different Types regarding their anatomical structure. Yet there are certain histological characters in the Araceae which I have shown to be constant and characteristic for distinct groups as a result of my extensive studies of fresh and dried material. I have been guided by these [characters] alone no more than by the leaf arrangement, the shoot architecture and the floral structure. If however they appear combined with other morphological characters, I have granted them due attention and so am now in a position to determine at least to which major group the plant must belong for any Araceae otherwise unknown to me, using [only] a small piece of a petiole or stem and with the help of a piece of the leaf blade. Also in the floral morphology of the Araceae there was still much to be done, granted that, as far as it can be regarded as complete, Schott had paved the way in an outstanding manner.

Finally I must note that it would have been quite impossible to have produced some results relatively quickly in the study of this difficult family, if I had not enjoyed friendly support from many people. I am especially indebted to Prof. Alexander Braun who assisted me not only with living material for morphological studies but also placed at my disposal a number of his own observations which are also emphasized in the following treatise. Similarly I owe to the friendship of Herr Vetter, Director of the Imperial Garden of Schoenbrunn a great amount of living material, and of Herr Kolb, the Inspector of the Botanic Garden of Munich. The generosity of Privy Councillor [Regierungsrath] Prof. Fenzl, who permitted me the use of the rich and still not fully utilized legacy materials of Schott, a collection of exquisite illustrations, unique of its kind, which comprises the results of forty years of zealous research. Here I should also thank Prof. Dr. Reichardt for his friendly support in the use of the above-named collection. Also to Prof. Dr. C. Koch, who next to Schott has done the most for knowledge of the species of Araceae, I owe the provision [Ueberlassung] of his collections and drawings. Alph. De Candolle greatly lightened my burden by communication of his notes on the literature of the Araceae. Apart from these individuals I am also indebted to Herren Ascherson, Boissier, Drude, Thiselton Dyer, Garcke, J. Mueller Arg., Maxwell Masters, E. Regel, Schweinfurt and Warming. The

Commented [s1]: Interesting contrast here, distinguishing systematic connection (morphological similarity?) and relationship connection (genealogical?)

Commented [s2]: What exactly does Engler mean by a "type"? It must be a distinct morphological cluster

Commented [s3]: 1805 – 1877

systematic monograph of the Araceae in de Candolle's collection of Monographs will appear in the next few years − in the following essays an outline is given of the general relationships which have been considered self-evident also in the systematic treatment. I have made public the natural System of the Araceae, which is to be seen as the result of my morphological studies, prior to [the publication of] the latter, in order to give the reader an overview of the studies and an idea of their goal.

Munich, 19 August 1876.

A. Engler

Natural System of the Araceae

In the following systematic, rather than analytical, overview of the Araceae, the subfamilies [Gruppen] and genera are arranged always in a way that provides an idea of the gradual reduction of the floral parts. This system allows it to be very clearly perceived that reduction of the floral parts must have occurred in several [verschiedenen]* subfamilies [Gruppen] and thus that Schott's classification, in which the major divisions are based on floral structure, is unnatural. My system of the Araceae would have been [turned out: ausgefallen] quite different if I had had the aim of providing a means of identification for botanists less familiar with the family. My purpose is different: in the following system all phylogenetic relationships [verwandtschaftlichen Beziehungen] between individual groups [einzelnen Gruppen] should be presented as clearly as possible, and hence the number of subordinate groups is larger than perhaps seems necessary at first sight. The Araceae are a family poorly represented in herbaria. It is therefore likely that [our] knowledge of its taxic diversity [der Formen] is still far from complete, as is demonstrated by the new genera which are being discovered [bekannt werdenden] almost annually. It is thus to be expected that some of the groups which presently contain only a few genera will be enlarged by one or several more. All citations are here omitted since these are to be found in my systematic monograph of the Araceae and here are of only lesser interest. In those cases where the [phylogenetic] derivation of one genus is very probably from another, their names are arranged in vertical rows. If on the other hand a common origin of the genera is supposed, their names are listed side-by-side. The generic names in parentheses refer to those of Schott or to genera proposed by him which at best can be accepted as subgenera.

[* Engler's emphasis]

1. Subfamily Pothoideae Engl.

Vascular bundles without laticifers [Milchsaftgefässe]. Ground tissue without ┤ shaped or H shaped cells ("intercellular hairs"). Leaf arrangement (phyllotaxy) various. Leaf blade usually reticulate, more rarely parallel. Flowers bisexual, with or without a perigon, rarely unisexual. Ovules anatropous.

Trib. I. **Pothoeae** Engl. Climbing shrubs. Reiteration shoots arising in the axils of several foliage leaves. More seldom forming sympodia (*Anadendron, Culcasia*). Primary lateral veins of the leaf blade almost parallel to one another, the rest reticulately joined, rarely also parallel (*Pothoidium*). Flowers bisexual, with or without perigon, or unisexual. Ovules anatropous. Seeds lacking endosperm and with a macropodal embryo.

Subtrib. 1. *Pothoinae* Schott. Leaves diverging at ½ [distichous]. Fllowers bisexual, usually: P_{3+3}, A_{3+3}, $G_{(3)}$ / G_1 or $P_{(x)}$ A_{2+2} G_1

Pothos L. *Anadendron* Schott
Pothoidium Schott

Subtrib. 2. *Heteropsinae* Engl. Leaves diverging at ½ [distichous]. Flowers bisexual. A_{2+2}, $G_{(2)}$.

Subtrib. 3. *Culcasinae* Engl. Leaves diverging at ½ (?). Flowers unisexual.
♂: A_{2+2}; ♀: $G_{(2+2?)}$.

Culcasia Beauv.

2. Subfamily Monsteroideae Schott em.

Vascular bundles without laticifers [Milchsaftgefässe]. Ground tissue with numerous tannin-containing cells and with ┤ shaped or H shaped cells, the ends of which penetrate into the intercellular spaces like hairs. Usually climbing shrubs with leaves diverging at ½ and in such a way that their sheaths and blades are antidromous (except *Spathiphyllum*). In genera with shortened internodes (*Spathiphyllum*) the leaf arrangement later deviates from ½ and becomes closer to 3/7; the leaves are then homodromous. Flowers bisexual, rarely with, more frequently without a perigon, usually dimerous. Ovules anatropous or amphitropous.

3. Subfamily Lasioideae Engl.

Vascular bundles with simple laticifers, rarely these anastomosing (*Syngonium*) by fusion as they form. Climbing, often aculeate shrubs with elongated internodes or perennial herbs with prostrate axes or with a tuber. Leaves spiral, usually 2/5 and homodromous, with charactersitic reticulate venation, sagittate or three-parted with much-divided segments. Flowers bisexual, dimerous or unisexual, with or without a perigon. Seeds lacking endosperm [eiweisslos]. Embryo macropodal.

4. Subfamily Philodendroideae Engl.

Vascular bundles with simple laticifers formed by fusion. Subshrubs with shortened internodes or climbing shrubs with elongated internodes. Shoots usually beginning with only a cataphyll [Niederblatt] and then developing one to several foliage leaves [Laubblätter], which are spirally arranged (divergence usually 2/5) and homodromous. (in shoots of individual *Philodendra* with only a cataphyll, a foliage leaf and an aborted spathe, the divergence sometimes approaches ½ and then antidromy sometimes occurs). Leaves with numerous parallel veins of I, II and III grade. Flowers unisexual, sometimes the females ones with staminodes, lacking a perigon. Stamens sometimes forming synandria. Ovaries not rarely polymerous (2 – 8 –locular). Ovules anatropous or orthotropous. Seed with endosperm [eiweisshaltig]. Embryo axile.

5. Subfamily Aglaonemoideae Engl.

As in the Philodendroideae, in the Dieffenbachieae the spiral [xylem] vessels frequently carry milky latex [Milchsaft]. Shoots building small sympodial stems. Ovules anatropous with a short funicle and the seed without endosperm and with a macropodal embryo.

6. Subfamily Colocasioideae Engl.

Laticifers strongly developed, richly anastomosing by fusion, the large vessels of the vascular bundles also frequently carrying milky latex. With a sometimes robustly developed simple or branched sympodium or a tuberous herb. Shoots developing several foliage leaves and the inflorescence following several cataphylls, several cataphylls rarely developed immediately before the inflorescence. Lateral veins of the second grade diverging from those of the primary grade at a not very acute angle, meeting in the middle between the primaries and forming a zig-zag collective vein; marginal veins distinctly developed. Spathe of the inflorescence usually with a distinctly formed tube, which encloses the female inflorescence and with a more expanded lamina which surrounds the male inflorescence. Stamens of the male flowers in two whorls, forming synandria which open by pores. Ovules more seldom anatropous, more commonly hemiorthotropous on a distinct funicle. Seed with endosperm and an axile embryo.

7. Subfamily Staurostigmoideae Engl.

Laticifer cells not anastomosing, forming rows on both sides of the phloem. Collenchyma forming a complete peripheral sheath; the individual bundles without collenchyma. Herbaceous plants with tubers. Shoots usually developing 1 – 2 foliage leaves after very few cataphylls, and then either the inflorescence immediately or after a few cataphylls. Spadix covered up to the apex with somewhat laxly arranged flowers. Foliage leaves simple or pedate or pinnate. Venation of the foliage leaves reticulate. The spadix bearing flowers up to the apex [sic!] and laxly flowered in the middle. Male flowers comprising two or one whorl of stamens which form a synandrium. Female flowers surrounded by staminodes. Ovules anatropous on a short funicle. Seed without endosperm and with a macropodal embryo.

8. Subfamily Aroideae Engl.

Laticifer cells as in the previous subfamily; but with collenchyma-type phloem on the outer side of the peripheral bundles; lacking a continuous sheath of collenchyma. Herbaceous plants with underground stemlets or for the most part with tubers. Shoots usually developing a limited number of foliage leaves after very few cataphylls and then the inflorescence, more seldom with cataphylls between the foliage leaves and the inflorescence. Foliage leaves linear to pedate, usually sagittate; venation of the foliage leaves usually reticulate. The upper part of the spadix usually without flowers and instead forming an often very substantial appendix. Male flowers only seldom comprising two whorls of stamens, more frequently with one whorl composed of two or three stamens, sometimes reduced to a single stamen. Female flowers sometimes with staminodes, more frequently without them, and usually reduced to only one carpel. Ovules more seldom anatropous, usually orthotropous. Seed with endosperm, with an axile embryo (by which it can always be distinguished from the Lasieae, Amorphophallinae and Staurostigmoideae).

9. Subfamily Pistioideae Endl.

Floating water plants. Laticifers lacking. Internodes very abbreviated; leaves spirally arranged, pilose, prior to flowering lying on the water, becoming upright at the beginning of flower development. The numerous, successive flowering shoots always

consist of a thin, membranous cataphyll, a foliage leaf and the inflorescence. Male flowers consisting of two connate anthers, forming a whorl. Female inflorescence single-flowered. Ovary one-locular, producing numerous sessile orthotropous ovules on the basal placenta. On the inflorescence axis there is an annulus between the male and female inflorescences which can be interpreted as either an expansion of the axis, like the sheath-wall of ***Ambrosinia***, or as a structure corresponding to an aborted male floral whorl. Seed with endosperm. Embryo small, ovoid.

10. Subfamily Lemnoideae Engl.

Floating water plants. Shoots beginning with a thin, membranous cataphyll (*Spirodela*) or without one (*Lemna*), bearing a single foliage leaf, that is not sharply separated from the axis which is broadened on either side by two sac-like structures. Spathe [Hüllblatt] of the inflorescence thinly membranous, terminating the shoot along with the inflorescence in one of the sac-like dilations, lacking in *Wolffia*. Male inflorescence reduced to two or one single –stamened flowers, the female inflorescence to a single ovary. Ovules orthotropous or anatropous. Seed with endosperm.