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Über den Entwicklungsgang in der Familie der Araceen und
über die Blütenmorphologie derselben. Bot. Jahrb. Syst. 5:
141 – 188, 287 – 336. Taf. I – V.

Translation by Simon Mayo (January 2011). Translator's note: This is a rough translation and as far as I know the first attempt to render this seminal work into English. Any corrections or improvements would be welcomed. Wherever I have considered it advisable I have added the German phrase (in original grammatical cases) in square brackets, e.g. [Entwicklungsgeschichte]. This is particularly important when words like *Verwandtschaft* or *Entwicklungsgeschichte* are concerned, because the context is important in these cases for the correct meaning. There are doubtless other cases in this text which I have missed. Wherever I have thought it necessary to add some comment or addition of my own, these are given in curly brackets, e.g. {and}. Any phrases within round brackets "(...)" represent parentheses made by Engler himself. The spelling and circumscription of taxon names is maintained as in Engler's original text.

12. On the course of evolution [Entwicklungsgang] in the family of the Araceae and on their floral morphology

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1. Introduction

When some years ago I published my treatment of the Brazilian Araceae and afterwards the monograph of the whole family in the continuation {series} of the Prodrromus (volume II), I proposed at the same time a system of the Araceae which diverged essentially from that of Schott, although the latter had established the scientific knowledge of the family. A large part of the tribes and smaller groups set up by Schott were however so natural that with a few alterations they could be maintained. Nevertheless, a thorough study of floral organization, shoot organization, {leaf} venation and anatomical structure showed me that a division {of the family} based exclusively on the floral organization could never lead to a natural grouping in this family, in which the flowers show themselves to be so polymorphic and inconstant. {Making a} Natural grouping does not consist of arranging the genera in such a way as to facilitate identification or accessibility for non-specialists, but rather the establishment of an arrangement which demonstrates most graphically the evolutionary pathways [den Entwicklungsgang] in the family. Since the representation of ancestors is thus sought, which is out of reach of direct observation, it is obvious that even the best “natural arrangement” must suffer shortcomings, while on the other hand, the worst artificial arrangement, which uses first one and then another conspicuous character, can escape blame for incorrectness so long as the classification is grounded on sufficiently demonstrated facts. Just as an artificial division can be based on the simple observation of macroscopic characters, it can also be so based on microscopically observed characteristics. Hence, the microscopist who does no more than present certain characters by means of manual skill has not the least ground for his work to be regarded as more meritorious than another botanist who only describes macroscopic characters. The introduction of anatomical characters into systematics is of no greater merit than that of any other character so long as it has not been tested to what extent {the consideration of } these anatomical characters are suitable to make a grouping that corresponds to the natural evolutionary pathway [Entwicklungsgang].

In the Araceae, which has proved to be a natural family partly through their similarity in structure and development, and partly through the interconnection of their varied forms, I had nevertheless discovered that certain anatomical characters recurred when the growth conditions varied in such a way that the individual parts of the plant had to fulfil other mechanical tasks. If I found that the climbing *Pothos* and related genera possessed neither laticifers [Milchsaftgefäße] nor trichosclereids [Spicularzellen], that the climbing *Monstera* and related genera in contrast did possess trichosclereids, and the climbing *Philodendron* had laticifers but no trichosclereids, then I had the right to regard these anatomical characters as appropriate for {the purposes of} systematics. I was persuaded {by the following observations} that in various taxonomic groups [Verwandschaftsgruppen] of the Araceae, the type of venation is heritable and has nothing to do with leaf shape. Thus, although the sagittate leaves of many Araceae possess reticulate venation, the sagittate leaves of the *Alocasias* are distinguished by the fact that the secondary lateral veins form a collective vein nearly parallel to the primary lateral veins, while on the other hand in the sagittate leaves of *Philodendron* and *Homalomena*, the secondary lateral veins have an almost parallel course. I also found that in lanceolate and ovate leaves of these genera the same rule for the venation still applied and this was the case also in those species with pedatifid or pinnatifid leaves. I was still more justified to assign a high rank to these characters in the natural grouping when I found that those derived from the venation and the ground tissue {i.e. anatomy} sometimes coincide. Finally I was quite sure of my case when I found that the genera brought together by the above-mentioned characters either agree in their floral structure or reveal a correlation in their variant forms [Verschiedenheiten].

Both in the *Flora Brasiliensis* and in the *Suites au Prodromus* of De Candolle, only limited space was available for me to set out the presentation of the general relations {of the classification}, but nonetheless I was able to depict ¹ in the *Flora brasiliensis* the most important anatomical Types and give in both works a short synopsis of the general relations. I had to postpone until later the {explanation of the} detailed reasons for my arrangement {of the taxa} and for the assertions² stated, as it were, in the arrangement {classification} itself.

¹ *Flora brasiliensis*. Vol. III. Pars II. Tab. 2 – 5.

² A valued colleague who had also perceived how well suited such a polymorphic family is to provide an idea of the predominant principles of organization of the Angiosperms and for stimulating a

The publication of my phytogeographic works laid claim to several years, in which I was able to collect together lasting material for further studies of the Araceae, but I was not able to provide a full account of their predominant laws of organization and developmental forms [Entwicklungsformen]. Now I am finally in a position to partially fulfil my obligations in this direction and to review at least the floral organization of the Araceae. This is a question of showing that the genera I have brought together into a group, insofar as they do not agree in their floral structure, nevertheless exhibit variant forms [Verschiedenheiten] whose origin {derivation} from other {kinds of} flowers can be explained by natural processes. Thus at best, series can be established which permit us to recognize the step-wise change of the individual components of the flowers. However, it depends on our {own} opinion whether we prefer {to interpret} these series as progressive [aufsteigenden] or regressive [absteigenden] successions.

As far as the illustrations are concerned, I would have had to provide ten times the number of plates in order to explain everything visually. I did not consider this necessary since Schott's *Genera Aroidearum*, a work of classic value, should be available in any large botanical library, and also my illustrations in the *Flora brasiliensis* provide a wealth of illustrative description. Thus I have here limited myself to presenting as illustrations only those cases which are important for theoretical consideration. Whoever wishes for more details on the family can obtain a comprehensive idea of the multiplicity of forms in this family from the "Araceae exsiccatae et illustratae"³ published by me.

The aim of treating plant families in a such a way that the phylogenetic relationships [phylogenetischen Beziehungen) within the family come to the fore is not as new as one sometimes thinks. Earlier morphologists and systematists, especially A. de Jussieu and A. St. Hilaire devoted themselves to such aspirations, with the difference however, that they did not always link to the word "relationship" [Verwandtschaft] - that was as familiar to them as to us - the idea of ancestry [Abstammung] or of mutual genetic connections [gegenseitigen genetischen Beziehungen]. In fact, today, {even} with our direct aim of establishing the genetic

comparative study, had made the Araceae a topic for a colleague. He made a thorough study of my works on the family and consequently, as he reported to me, came to recognize that reduction played an important role in the formation of the flowers in Araceae. The same colleague, however, often declared that he was still waiting for the detailed evidence of my expressed assertions.

³ See Bot. Jahrb. IV, Beiblatt Nr. 4 and V, Beiblatt Nr. 6

connections within a family, we also get no further than the recognition that some genera are more closely “related” and others stand further apart. However, the establishment of truly genetic connections is {thus} only very weakly made and in fact one must often be satisfied if it is possible to state with confidence that this genus belongs to a phylogenetically older “Type” and that to a phylogenetically younger one. Furthermore, the phylogenetic trees [Stammbäume] that have been constructed here and there, which only extremely seldom were set up with the presumption that they should express exactly the evolutionary development [Entwicklung] that actually happened, serve rather to show that one genus belongs to a phylogenetically older stage and another to one phylogenetically younger. Now, in reality, however, there often arises vagueness about what is to be regarded as an ancient [ältere] structure [Bildung] and what a more recent one. Moreover, more recent investigations have often showed that not rarely, external correspondences {of characters between taxa}, which lead erroneously to the acceptance of relationship, are no more than adaptations brought about by the same cause at different times. Younger systematists have also often paid heed to this {question} in their monographic treatments (but indeed only such {kinds of study} could be successful in this regard [solche können ja auch nur allein in dieser Beziehung zum Ziele führen]), but rather incidentally and not always with a clearly stated intention to sharply separate characters resulting from adaptation from those which are phylogenetic or hereditary. With regard to the vegetative organs, in which the adaptations are often clearly evident even to laymen, one is in less danger of mistaking adaptations for phylogenetic phenomena than of neglecting them far too much when establishing phylogenetic relationships. It is of the greatest significance for Morphology and Systematics that von Nägeli, the doyen of modern botany, who has made epoch-making investigations in almost all disciplines of our science and stands unequalled among botanists for his logical rigour, has undertaken⁴ to elucidate the phylogenetic laws of the plant kingdom and particularly to emphasize the features brought about through adaptation (as a result of external stimuli) in contrast to those forms of organization produced by inherent causes. The inner causes, just as outer ones, produce form changes in different parts of the plant. In one plant, the form of a certain part can be phylogenetically more advanced and in the form of another part more retarded than in another plant. It is thus immediately apparent that

⁴ Von Nägeli: Mechanisch-physiologische Theorie der Abstammungslehre. München 1883.

in comparing numerous plants of a higher stage of development/evolution [Entwicklungsstufe] the establishment of the phylogeny [phylogenetisch Entwicklung] encounters considerable difficulties on account of the large number of parts to be compared. Nevertheless, the phylogenetic pathway [phylogenetische Entwicklungsgang] is more likely to be discovered in those families in which a great diversity of forms particularly of the reproductive organs, occurs, at least in broad outline, rather than in those that present a general uniformity in floral structure. The ascertainment of the ontogenies [Ontogenien]⁵ is of great significance for the description of phylogenetic advancement, or simply, progression, and especially interesting are those cases in which the development stages [Entwicklungsstufen] of less advanced plants can be recognized in the ontogeny of an advanced plant. The Araceae family is however rather rich in such forms and hence the establishment of the resulting progressions is here and there facilitated.

⁵ It is very worthwhile here to give an opinion about what ontogenetic development [Entwicklungsgeschichte] can and cannot achieve, from the pages of a botanist who in this field has achieved such prominence and who has first laid the foundations for so many methods. Thus states von Nägeli loc.cit. p. 455: "The {study of} ontogenetic development [Entwicklungsgeschichte] forms only the first step and the indispensable prerequisite for reaching a causal understanding. It is not yet, as has often been overlooked, the fulfilment of that general demand. For if I know precisely how [wie] something has arisen, I do not yet know on this account why and by what means [wodurch] it has come about." One should point out that the above-mentioned pursuit {to comprehend} the development of an individual does not give the required understanding. "*In order to grasp the genetic significance of any feature it must be retraced along its ancestral succession to where it began.* If this can be done with the aid of observation, then it is possible to discern the origins {causes?} of the feature, whether innate or external. At the time that ontogenetic development [Entwicklungsgeschichte] was not yet a {scientific} discipline, one sought to determine the systematic significance of a feature by comparative morphological examination of completed stages [states, Zustände] and here C. Schimper, A. Braun and Wydler have obtained especially valuable results. Since *ontogenetic development* [Entwicklungsgeschichte] was then pursued not only in a deliberate way as a scientific challenge, but rather *unconsciously as a fashion*, it often came into conflict with the earlier comparative morphology. *Instead of combining the two methods in a rational way, the younger workers [die Neuerer] believed that the ontogenetic development [Entwicklungsgeschichte] alone sufficed and that they could ignore the comparative treatment, which also required more knowledge, more work and reflection.*" — Sapientia sat. On p. 457 it is further reported that: "it would be a thoughtless presumption if one went further and wished to establish, in opposition to comparative morphology, systematic evolutionary relationships [verwandtschaftliche systematische Beziehungen], which are only provided by the phylogenetic significance of the Types [Baupläne]." (It is as well to take note that this concerns only the Phanerogams). "The observation of a primordial protuberance of cell tissue {?meristem?} does not even grant us a complete ontogenetic development history [Entwicklungsgeschichte], in that the latter can arise in various ways from the initial cells and thus have dissimilar ontogenetic significance." This is then further elaborated. "There are all these undeniable possibilities, and it cannot be doubted that sometimes one and sometimes the other corresponds to the actual fact. Whether and to what extent they are to be taken into consideration must be established by a *comparative method*, which essentially can only be a phylogenetic one, and as is self-evident, by considering all relevant facts {and} with the greatest caution and avoidance of arbitrary hypotheses". When one considers that such works as that of Huisgen on the placentas could emerge from a botanical institute, then one will find these statements well grounded and not too harsh. It is also characteristic how few younger botanists have the inclination to undertake extensive morphological investigations on major taxa [auf grösseres Material].

2. Progressions {= transformation series} in the formation of the tissues

If one compares the anatomy of the stems and petioles or also the leaf ribs of various Araceae {occurring} *in the same growth conditions*, one will frequently encounter great differences. These are important in regard to the distribution of the mechanical elements. Since, however, in the latter one often runs the risk of bringing adaptive phenomena into the realm of phylogenetic features, I will leave these out of our consideration and consider only those differences which occur in the ground tissues or in the phloem [Leptom] of the vascular strands, and which also already make their presence felt in the young stages of the plant. The following stages can be distinguished:

Stage I. The ground tissue possesses either no tannin-containing, tubular cells [Gerbstoff führenden schlauchförmigen Zellen] or if these are present they are irregularly scattered and have no connection with the vascular bundles. Trichosclereids [Spicularzellen] and lactiferous vessels [Milchsaftgefäße] absent. *Pothos, Culcasia, Heteropsis, Anadendron, Anthurium, Acorus, Gymnostachys, Zamioculcas, Gonatopus.*

Stage II. The ground tissue either lacks tannin cells [Gerbstoff führenden Zellen] or when these are present (e.g. abundantly in *Rhodospatha heliconifolia*) they are irregularly scattered and not associated with the vascular bundles. Lactiferous vessels [Milchsaftgefäße] absent; in contrast the ground tissue is richly permeated with long, two-armed or H-shaped trichosclereids [Spicularzellen], which extend much beyond the other ground tissue cells and grow into the intercellular spaces. *Spathiphyllum, Holochlamys, Rhodospatha, Stenospermation, Monstera, Scindapsus, Epipremnum, Rhapsidophora.*

Stage III. The ground tissue either lacks tannin cells [Gerbstoff führenden Zellen] or they are irregularly scattered, and never possesses trichosclereids. In addition, lactiferous vessels [Milchsaftgefäße] are found on the border of or within the phloem [des Leptoms], which individually have a definite position.

- a. The lactiferous vessels form straight rows. — All known Araceae apart from those mentioned in b. below.

- b. The lactiferous vessels form lateral branches and anastomose. —
Colocasia, Alocasia, Caladium, Xanthosoma, Remusatia?, Gonatanthus?, Syngonium.

Most Araceae have reached the third stage, and within these many different variations are evident, which I will go into in a later paper that is to be dedicated specially to the anatomical relationships of the Araceae {this seems never to have been published}. Since the three major types [Hauptverschiedenheiten] of the tissue of Araceae are observed already in young plants, all plants which stand at the second stage must be more closely related phylogenetically to one another than to one of the third stage and likewise those of the third stage be more closely related to one another than to one of the second stage. It is however further apparent that it is only out of the first stage that the other two can each be derived independently [jede für sich] so that thus the second stage and the third stage stand in the same relation to the first.

3. Leaf venation

As in all plants, the venation of the foliage leaves is related to their shape. However, one finds very often that leaves of the same shape have different venation. For example, if one compares the cordate leaf of a *Philodendron* with the cordate leaf of an *Anthurium* or with the cordate leaf of a *Colocasia*, or the lanceolate leaf of a *Philodendron* with the lanceolate leaf of an *Anthurium*, or the pinnatifid leaf of a *Philodendron* with the pinnatifid leaf of an *Anthurium*, or a *Monstera* or a *Rhaphidophora* and then a *Schizocasia*, or the pedatifid leaf of an *Anthurium* (*Anth. pedatum* Kunth) with the pedatifid leaf of a *Sauromatum*, *Typhonium* or a *Xanthosoma*, then one will satisfy oneself that even when the shape is similar, the venation is different, while on the other hand, the venation is subject to the same rule in the same genus or within closely related genera even when the leaves are of different shape. On these grounds I regard it as justifiable to accept this transformation series [Progression] as based on inherent causes.

Progressions {transformation series} in leaf venation

Stage I. The primary lateral veins, mostly not numerous, are nearly parallel to one another in the whole leaf or within individual leaf segments, while the secondary

and tertiary veins form a network between the primary ones; only in linear leaves do the secondary and tertiary veins run nearly parallel. — This is the case in the greater part of the Araceae and also in histologically distinct taxa.

Stage II. The primary lateral veins, mostly not numerous, are nearly parallel to one another within the whole leaf or within individual leaf segments. From the secondary lateral veins arises one which takes its course, approximately in the middle between the primary lateral veins, as the collective vein for most of the rest of the secondaries and for the tertiary veins. — *Colocasia, Alocasia, Steudnera, Gonatanthus, Remusatia, Schizocasia, Syngonium, Porphyrospatha, Ariopsis.*

Stage III. The numerous primary lateral veins are nearly parallel to one another and also the secondary veins often run parallel to them; but the tertiary and quaternary veins, or the secondary, tertiary and quaternary veins form a network between the major veins. There are intermediate forms between this stage and stage I. — *Spathiphyllum, Holochlamys, Rhodospatha, Stenospermation, Monstera, Scindapsus, Epipremnum, Rhapsidophora.*

Stage IV. The numerous primary, secondary and tertiary veins are nearly parallel to one another. Between these veins run transverse or oblique, fine transverse veins. — *Richardia, Peltandra, Typhonodorum, Homalomena, Chamaecladon, Schismatoglottis, Bucephalandra, Apatemone, Philodendron, Philonotion, Adelonema, Anubias, Algadorum. Dieffenbachia* and *Aglaonema* also belong here to some extent, but intermediate forms occur in these genera with Stage III.

The relationship of these stages to one another is different from the anatomical structure, where stages II and III distinguish themselves from stage I in that some new {character} was added. Here, on the other hand, we find that the stages are only different in so far as the lateral veins depart from their relatively major veins by a more or less acute angle. {Thus} here each stage can be transformed into the other without adding any new {character}. On this account, the venation cannot be {regarded} as of such great significance as the histological conditions.

4. Leaf shape

The extraordinarily varied leaf forms of the Araceae are to be attributed partly to adaptation and partly to inherent causes. For assimilation, which the leaves carry out, it is the same whether the leaf blade, turned towards the light, has an ovate,

cordate, pedatifid or pinnatifid shape so long as the surface area remains the same. It is furthermore of no consequence whether assimilation is carried out by several small leaves or by a large extended leaf, so long as the assimilation surfaces are the same. Under otherwise identical conditions we find that when the leaf blade is smaller the number of leaves is greater, and when the blade is larger the number of leaves is less (compare for example *Biarum* and *Arum* on the one hand and *Arisaema* and *Amorphophallus* on the other). This is easily explained by the fact that in the development of small leaf blades, enough material is available for new leaves, whereas in the development of larger leaf blades there is only enough for one or a few leaves.

Adaptations in the shape of leaves

If plant growth [die Vegetation] takes place below ground for part of the year, then the first leaf primordia of the shoot change into cataphylls [Niederblättern], that is, the development of the blade does not take place, which in fact is also frequently indicated here and there by cataphylls occurring adjacent to foliage leaves. First the latest leaves develop a blade. That, however, immediate influences on the plant are not the cause of the blade's appearance [die Ursache der Spreitenanlage] arises from the fact that below the soil the complete construction of the blade takes place, but only later does it expand. Indeed, the foliage leaves can only be formed [können ...angelegt werden] under the protection of other leaf organs. The cataphylls which precede the foliage leaves are found within the protection of the leaf sheath in the axil from which they arise. The immediate cause of this development is thus neither the protection which the foliage leaves receive when they are forming, nor is subterranean growth the immediate cause of cataphyll formation, at least not in the sense that a removal to other conditions would bring about a different development (excepting the cataphylls immediately preceding the foliage leaves). The present normal state has gradually come about because the same stimulus has been repeatedly asserted, and thus such an adaptation can then only reappear in the previous form if the earlier conditions act repeatedly during a long period of time [Der jetzt zur Regel gewordene Zustand ist allmählich zu Stande gekommen, dadurch dass dieselben Einflüsse sich wiederholt geltend machten, es kann daher eine solche Anpassung auch erst dann wieder in die ältere Form zurückkehren, wenn die früheren Bedingungen wiederholt durch lange Zeiträume einwirken]. However, the fact that in general a change, a

reversion due to external influences, is conceivable shows that we have before us an adaptation rather than a phylogenetic progression {This seems to show the influence of Nägeli's orthogenetic theory; adaptations are secondary to the main phylogenetic progression which is the result of different, orthogenetic forces}. If the reproductive shoot develops in the same year, then the number of cataphylls that precede the foliage leaves is less (*Spathicarpa*). But if on the other hand the reproductive shoot only comes to full development in the following year, then the number of such cataphylls is greater. It often happens that a shoot needs several years to reach the flowering state and in this case cataphylls alternate with foliage leaves. If the blade of the foliage leaves is very big, as in *Dracontium*, *Hydrosme* and *Amorphophallus*, then only a single foliage leaf follows after several cataphylls.

When growth takes place always on the surface of the ground then in individual shoots always only a few, at most no more than two, cataphylls precede the foliage leaves.

Progressions {transformation series} in leaf shape

Stage I. Leaves not divided into petiole and blade. — *Acorus*, *Gymnostachys*.

Stage II. Leaves divided into petiole and blade. Blade undivided, narrower at the base than in the middle. — *Pothos*, many *Anthurium*, etc.

Stage III. Leaves divided into petiole and blade. Blade outline cordate, sagittate, hastate as a result of stronger growth at the base.

- a. Blade undivided.
- b. Blade, as a result of locally discontinued growth, perforated or pinnatifid through the fusion of perforations lying next to one another and between two major veins. — *Monstera*, *Rhaphidophora*, *Epipremnum*, *Dracontium desciscens*, *Anchomanes*.

Stage IV. Leaves divided into petiole and blade. Blade outline cordate to sagittate, and moreover racemosely branched. The branches of the blade [Auszweigungen] seem to originate nearly simultaneously, since sometimes there are signs of basipetal development, in that the lowermost segments [Abschnitte] are more united with one another because less divided. This closer cohesion of the lower segments also permits the idea that the primary basal segments have divided dichotomously.

- a. Blade lobed. — *Anthurium*, *Philodendron*.

- b. Blade pinnatifid. — *Philodendron*, *Schizocasia*.
- c. Blade pinnate. — *Zamioculcas Loddigesii*.
- d. Blade bi- or tri-pinnatifid. — *Philodendron bipinnatifidum*.
- e. Blade bipinnate. — *Gonatopus Boivini*.
- f. Blade palmatisect, the lower segments more or less cohering. — *Anthurium sinuatum*.
- g. Blade palmately cleft, but the lower segments cohering with one another, all segments pinnatifid or bipinnatifid. — *Anchomanes*, *Dracontium polyphyllum*, *Hydrosme*, *Amorphophallus*.
- h. Blade digitate, the individual leaflets deciduous [abfällig] {these leaflets are not deciduous!! This must be an error on Engler's part}. — *Anthurium digitatum*, *A. variable*, several species of *Arisaema*.

Stage V. Leaves divided into petiole and blade. Blade clearly cymosely branched, the bases of the lateral segments separate from one another, and thus the leaf is decidedly pedatifid. — *Xanthosoma*, *Syngonium*, *Sauromatum*, *Syngonium*, *Typhonium*, *Dracunculus*, *Helicodiceros*, *Helicophyllum*.

The connection of these stages and their progression [der Fortschritt derselben] in the above series can be verified in some cases by the ontogeny in one and the same plant. So for example, we find that in *Anthurium digitatum* and *Anth. variable*, the leaves of the young plants at Stage IIIa, and those of the older plants at Stage IVh. In *Anthurium sinuatum* the Stages II, IIIa, IVf develop sequentially in the same plant. All *Philodendron*, even if they have reached Stage IVd in their leaf development, express Stages II or IIIa in their youngest stages. In *Anchomanes dubius* and *A. hookeri* we can observe [constatiren] Stages III, IIIb, IVg from the seedling onwards. *Sauromatum* exhibits Stages IIIa and V, as do *Syngonium peliocladum*, *Dracunculus*, *Helicodiceros* and *Helicophyllum*. In a word, no matter how much the leaf of an Araceae later becomes divided, the leaves of the young plants belong to Stages II and III. Furthermore similar [phenomena] can be demonstrated just as well in many other families.

5. Shoot organization [Sprossbildung]

Here are easily found both adaptation and transformation series [Progressionen], which can be distinguished without difficulty.

Progressions [transformation series] in shoot organization

Stage I. Branching is from every angle, whether the shoot is subterranean or above-ground; buds can arise in the axil of every leaf. — *Acorus*, *Pothos pr.p.*, *Anthurium*, *Monstera*, *Philodendron*; but only until they come into flower.

Stage II. Branching takes place with preference for certain shoots determined by their position; but the shoots bear an indeterminate number of leaves. — The great majority of Araceae are thus, in which growth is sympodial and the continuation shoot [Fortsetzungsspross] of the sympodium arises always in the axil of leaf ($n - 1$), i.e. the penultimate leaf preceding the spathe.

Stage III. Branching takes place with preference for certain shoots determined by their position; the shoots bear a determinate number of leaves.

- a. The continuation shoots develop only two cataphylls, one foliage leaf and a spathe with inflorescence. — *Anthurium*.
- b. The continuation shoots develop only one cataphyll, one foliage leaf and the inflorescence. — *Philodendron*, *Cryptocoryne*, *Pistia*.

In those plants with a determinate number of leaves in the continuation shoots we always find accessory shoots [Beisprosse], in *Anthurium* usually in the axil of the cataphyll ($n - 1$) or of the second leaf of the shoot, and in *Philodendron* and *Pistia* usually in the axil of the cataphyll ($n - 1$) or of the first leaf of the shoot. — Further details on this and on other shoot organization of the Araceae [are to be found in] my treatment: Vergleichende Untersuchungen über die morphologischen Verhältnisse der Araceae. — Nova Acta d. Leop. Carol. Akad. XXXIX. Nr. 3 and 4 (1877).

Adaptations in shoot organization

The branching systems develop either upright and above-ground, shrub-like or climbing, or creeping, procumbent {or} subterranean with more or less elongated internodes.

The branching systems form either above-ground a sympodial stem with abbreviated internodes (*Philodendron Selloum*, *Anthurium Olfersianum*, etc., *Dieffenbachia*) or underground a sympodial rhizome or a tuber.

In the axils of the basal leaves of *Xanthosoma* species and *Colocasia Antiquorum* sometimes several buds develop next to one another, {and} on the stolons of *Remusatia* and *Gonatanthus* numerous buds arise which become detachable bulbils. At the junction of the leaf blade and petiole tubercles develop in *Amorphophallus bulbifer* {and also} in *Pinellia tuberifera* and *Typhonium bulbiferum* at the junction between sheath and petiole, which after the withering of the leaf remain in the soil and grow into new plants. In *Zamioculcas Loddigesii* the individual leaflets fall off and produce at first at their base a tuberous swelling on which a new shoot arises (see Bot. Jahrb. I, p. 189).

6. The spathe

In the development of {the spathe} there is also a number of phenomena which are considered to be transformation series [Progressionen], while the absence or presence of colour in the spathe is simply an adaptation which, however, constantly happens in similar environmental conditions [äusseren Bedingungen].

Progressions {transformation series} in spathe development [Entwicklung]

Stage I. The spathe is only a little different from the preceding leaves.

- a. The spathe is similar to a foliage leaf and united only at the base to the peduncle, which it encloses in the young stage. — *Orontium*.
- b. The spathe is similar to a foliage leaf and is united to the peduncle up to the base of the inflorescence, which it does not envelop. — *Acorus*.
- c. The spathe is bract-like [hochblattartig], is situated at the base of the inflorescence, and protects it but only in the youngest stages and is assisted in this function by numerous preceding bracts (*Gymnostachys*) or foliage leaves (*Pothodium*).

Stage II. The spathe is bract-like, green, colourless or coloured, envelops the spadix in the young stages, but then spreads out or reflexes and leaves the inflorescence free.

- a. The spathe is united with the petiole up to the base of the inflorescence, but sometimes becomes free below the inflorescence. The flowers are in the following states:-

1. Flowers with a perigon and bisexual. — *Pothos*, *Anthurium pr. p.*,
Spathiphyllum pr. p.

2. Flowers without a perigon and bisexual. — *Rhodospatha*.

3. Flowers without a perigon and unisexual. — *Nephtytis*,
Oligogynium.

b. The spathe is united with the whole dorsal side of the inflorescence and is spread out at the end of flower development. — *Spathicarpa*,
Spathantheum.

Stage III. The spathe is bract-like, green, colourless or coloured, tightly envelops the spadix in the young stages and later also surrounds the spadix, but at a greater distance from it. There is no constriction. Also here the individual flowers exhibit a variable structure [Verhalten]:

1. The flowers are perigoniate as in I and IIa. — *Symplocarpus*, *Ophione*,
Echidnium, *Dracontium*, *Urospatha*, *Cyrtosperma*, *Lasia*, *Anthurium pr.p.*,
Spathiphyllum pr.p., *Holochlamys*, *Anadendron*.

2. The flowers are naked but bisexual. — *Calla*, *Scindapsus*, *Cuscuaria*,
Epipremnum, *Rhaphidophora*, *Monstera*, *Heteropsis*, *Amydrium*,
Anepsias, *Stenospermation*.

3. The flowers are naked and unisexual. — *Aglanema*, *Aglaodorum*,
Culcasia, *Montrichardia*, *Anubias*, *Ariopsis*, *Anchomanes*, *Synantherias*,
Plesmonium, *Arisarum*, *Theriophonum pr.p.*, *Homalomena* (which shows a slight {spathe} constriction).

Stage IV. The spathe is bract-like, green, colourless or coloured, tightly envelops the spadix in the young stages and later lies closer to the lower part of the inflorescence than to the upper part. The flowers are naked and unisexual. —
Staurostigma, *Taccarum*, *Zantedeschia*, *Hydrosme*, *Amorphophallus*, *Ambrosinia*.

Stage V. The spathe is bract-like, green, colourless or coloured, lying close to the spadix in the young stages and in one or two places is strongly constricted, so that a tube-part [Röhrentheil] and a blade [literally “flag-part” Fahnenheileil] can be distinguished. Flowers always unisexual.

a. The constriction occurs at the upper limit of the inflorescence and is usually overtopped by the spadix appendix.

1. No appendix on the spadix. — *Stylochiton*, *Cryptocoryne*,
Lagenandra.

2. Spadix ending in an appendix. — *Arum*, *Biarum*, *Theriophonum*, *Helicophyllum*, *Helicodiceros*, *Dracunculus*.

b. The constriction occurs below the fertile male inflorescence.

1. The constriction is only weak. — *Peltandra*, *Anubias*, *Sauromatum*.

2. The constriction is in itself weak, but on the inner side is reinforced by a prominent, ring-like transverse ridge. — *Pinellia*.

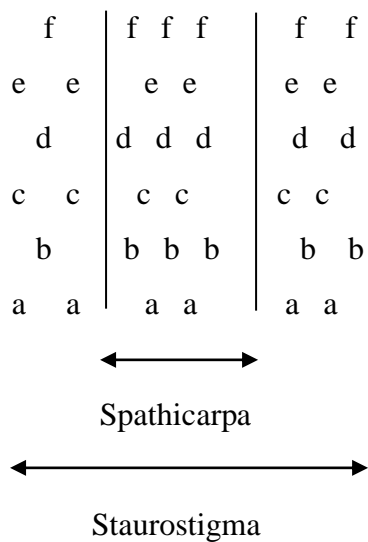
3. The constriction is strong and the lower tube part of the spathe [Scheide] remains persistent during fruit ripening or becomes enlarged. — *Typhonium*, *Remusatia*, *Gonatanthus*, *Colocasia*, *Alocasia*, *Caladium*, *Xanthosoma*, *Syngonium*, *Philodendron*, *Philonotium*, *Schismatoglottis*, *Piptospatha*, *Microcasia*, *Rhynchopyle*, *Dieffenbachia*.

7. The spadix

In relation to that of other families the inflorescence of the Araceae is very uniform. As in the inflorescence of the Leguminosae, which in spite of the restriction to inflorescence types derived from the raceme, still develops in many different ways, so we find in the Araceae many different grades even though the inflorescence is always a spike or spadix.

Apart from a few developmentally deviant forms [Bildungsabweichungen], in which branching occurs at the base of the spadix, the inflorescence is a spike with bractless flowers. The arrangement of the flowers is spiral in most inflorescences, but also in many cases in whorls. There are few cases of spirally arranged flowers which are also situated distantly from one another; this is the case only in *Pothos remotus* and a few of its relatives, and in *Arisarum* and some *Arisaema* (in the male inflorescence). Otherwise the flowers are always densely packed, so that we can see most clearly the parastichies standing out. Nevertheless the whorled arrangement is also quite common; in some cases the parastichies are very steep {at a high angle} but the flowers are still not completely whorled, e.g. in *Arum Dioscoridis*. Spadices with whorled flowers behave the same as those with spiral arrangement, as those of *Aquilegia* {compared with} those of *Helleborus*. I found completely whorled arrangement for example in the inflorescence of *Biarum tenuifolium*, which is illustrated in Plate IV, Fig. 42. We also find whorled arrangement in *Lagenandra* and

Cryptocoryne, where however the number of whorls is reduced to one. Also decidedly whorled are the flowers in the spadix of *Staurostigma Luschnathianum* where the individual whorls are divided into six parts (see Plate IV, Fig 47) {this reference is erroneous, the figures of this species are on Plate I}. The relationship of the flowers to one another is interesting in *Spathicarpa sagittifolia*; in young spadices we see quite distinctly tripartite and bipartite semi-whorls alternating with one another and the bipartite semi-whorls consist always of 2 male flowers, the tripartite semi-whorls consisting of two laterally positioned female flowers and one male flower situated in the middle. Only right at the base where there is less space do we see the tripartite semi-whorls replaced by bipartite ones (see Plate II, Figs. 17 – 18). Now, the genus *Spathicarpa*, as we will see later, is closely related to *Staurostigma*. If we disregard the sexual differentiation of the flowers, it becomes immediately clear from the comparison of the inflorescences of both genera that here there is the same basic arrangement of the flowers and that the number of orthostichies in *Spathicarpa* has turned out fewer because the slender spadix is fused dorsally to the spathe. The mechanical influence of the spathe makes itself felt only in so far as in the two outer orthostichies of the female flowers, the staminodes, which would have been situated on the outside, have not developed because of the pressure brought to bear by the inrolled spathe. The following diagram shows the relationship of the two inflorescences to one another quite clearly.



If the aim was only to clarify the development [Entwicklungsgeschichte], the whole inflorescence would be no more than a dorsiventral structure. Only the comparison explains its true nature. In *Staurostigma* the spadix becomes more slender upwards; in fact what we find here linked to this is a diminishing number of whorls; in that if a single flower lies over two spaces at once [indem sich über 2 Lücken auf einmal eine einzige Blüte lagert], then a 5-partite or 4-partite whorl will follow a 6-partite one. However, in very many cases it may be observed that the reduced thickness of the spadix does not result in the reduction in number of the parts of a whorl or cycle, but instead the layout of the flowers simply becomes smaller in the same degree as the floral axis which bears them becomes thinner. Thus in *Biarum tenuifolium* we see in the male inflorescence, in spite of the variable thickness of the spadix in its different tiers, the same number of whorl elements. Also in other Araceae from the *Aroideae* Group we can see the parastichies continue symmetrically through inflorescence tiers of different thickness; if they {the parastichies} become steeper on the thinner portions {of the spadix}, they lie in such a way that a transverse section through the floral rudiments situated on the thinner parts is more slender and that these floral receptacles are very often strongly elongated. In this discussion of the flowers of the *Aroideae* some cases of this type may be highlighted [Auf einzelne Fälle dieser Art ist bei der Besprechung der Blüten der *Aroideae* aufmerksam gemacht]. However, there is also no lack of cases, indeed in this same Group, where the parastichies are interrupted and thus their divergence [Divergenz] has been altered in consequence of the marked increase in {their} length.

I have been able to investigate very young primordia of not a few inflorescences of *Spathicarpa sagittifolia* but I always found simultaneous appearance of entire flowers and hence I cannot attribute developmentally the whorled arrangement in some Araceae to {the idea} that the establishment of the lowermost whorl necessarily gives rise to further primordial whorls. I also encountered in the youngest spadix stages of *Arum maculatum*, *Arisaema ringens* and *Ariopsis peltata* simultaneous development of the flowers. The transition from spiral to whorled arrangement can indeed only be explained by internal factors, as von Nägeli holds.

If we now disregard the spiral or whorled arrangement of the flowers, we can observe in the spadices progressions [Progressionen] of another kind which fall into the following sequence.

Progressions {transformation series} in the development [Ausbildung] of the spadix

Stage I. The spadix is uniformly covered with bisexual flowers up to its apex.

— *Pothos*, *Anthurium*, *Monstera*, *Spathiphyllum*, etc. etc.

Stage II. The spadix bears flowers up to the apex, but these are unisexual.

a. The lower flowers are female and the upper male; there is no naked space between male and female inflorescence {zones} but instead occasionally bisexual flowers. — *Staurostigma*, *Taccarum*, *Zantedeschia*, *Peltandra*, *Aglaodorum*, *Aglaonema*, *Chamaecladon*, *Homalomena*.

b. The lateral flowers are female and those of the central rows are male: *Spathicarpa*.

Stage III. The spadix bears unisexual flowers up to the apex, but one zone of floral primordia does not undergo sexual development, but bears only staminodes and pistillodes.

The staminodial flowers are situated between the male and female inflorescence {zones}.

1. The spadix zone covered with staminodial flowers is about as thick or thicker than the female or male inflorescence. — *Anubias*, *Philodendron*.

2. The spadix zone covered with staminodial flowers is thinner than the fertile female or male inflorescence⁶. — *Caladium*, *Xanthosoma*, *Syngonium*, *Remusatia*, *Philonotion*.

Stage IV. The spadix is covered with rudimentary floral receptacles [Blütenanlagen] or with staminodial flowers below and above the male inflorescence {zone} or only above it. — *Schismatoglottis*, *Bucephalandra*, *Microcasia*, *Piptospatha*, *Rhynchopyle*, *Alocasia*, *Helicodiceros*, *Arisaema ornatum*, *Typhonodorum*, *Mangonia*.

Stage V. The floral receptacles of upper half of the male inflorescence {zone} do not become differentiated but form an undifferentiated clavate, cylindric or tail-like appendix. — *Arum*, *Typhonium*, *Sauromatum*, *Arisaema*, *Amorphophallus*, *Hydrosme* etc. etc.

Stage VI. The spadix is sporadically naked [blütenlos] between female and male inflorescence {zones}. — *Dieffenbachia*.

Stage VII. The spadix is entirely naked [nackt] between female and male inflorescence {zones} and there are few female flowers⁷: *Ariopsis*, *Cryptocoryne*, *Stylochiton*.

Stage VIII. The spadix is entirely naked [nackt] between female and male inflorescence {zones} and female inflorescence is reduced to a single flower: *Ambrosinia*, *Pistia*.

Although there can be no doubt that this series indicates a stepwise progression, one could question on the other hand whether it would not be more correct to arrange the stages of the series in the reverse order, for we previously always found a progression therein which added something new to the existing attributes [denn wir fanden vorher immer einen Fortschritt darin, dass zu den bereits vorhandenen Eigenschaften neue hinzukamen]. We see, for example, that a poorly nourished *Anthurium* {plant} which has not yet attained full size develops small spadices with

⁶ One is easily inclined to the view that the atrophy of the flowers between male and female inflorescence {zones} is to be attributed to the pressure exerted in this place by the constricted spathe; however, there are many inflorescences in our family (e.g. *Sauromatum*, *Typhonium*), where floral rudiments are situated between male and female inflorescence {zones}, which only achieve a weak development and furthermore the spathe is not constricted at this place. Thus neither the spadix constriction can be always attributed to the spathe constriction, nor can it be affirmed that the spathe clings to the spadix constriction and by this means must itself become constricted.

⁷ Here we have in fact the naked inflorescence axis without any covering of rudimentary floral receptacles.

few flowers, but the same plant, if better nourished and having attained greater size, produces a two- to three-times larger spadix with many flowers. Furthermore we find in the inflorescences of *Pistia Stratiotes* sometimes only four 1-androus male flowers and sometimes five to eight. Should we then not suppose that inflorescences with numerous female and male flowers have developed {presumably Engler means here developed phylogenetically} from inflorescences with few female and male flowers? I do not believe so; for in these mentioned cases we are dealing merely with phenomena of development that depend on external influences and indeed quite immediate ones. The phylogenetic [phylogenetische] state which is in question in the inflorescence of *Anthurium* is not the number of flowers but rather that they are bisexual, perigoniate and arranged with no space in between them, and the phylogenetic state of the inflorescence of *Pistia* is characterized so that one female flower has very definite position in relation to a few favourably located staminate flowers. This position relationship is complex with a strongly developed division of function, {as} any additional lateral pistil would prejudice the already favourable {positional} relation where a stigma lies immediately behind the spathe opening. Similarly all the stages II – VI show a division of function and indeed an increase the higher is the stage number. The number of fertilizable pistils [zu befruchtenden Pistille] is always smaller than they would be in the same length of a spadix of stage I, and the number of ripening stamens is similarly smaller; but stamens and pistils stand in the same relation of position which we also find in all other monoecious inflorescences and which for fertilization is very favourable. When the spadix appendix is developed, the division of functions is advanced in such a way that a portion of the fused floral receptacles is employed as a guide for the insects; I say explicitly “is employed” because I see the primary cause for this development not in the breeding [Züchtung] of the insects but rather I conclude that the production of male flowers was initially excessive and gradually restricted itself to the appropriate consumption. Another portion of the rudimentary floral primordia are known to be employed for the partial closure of the spathe tube which surrounds the female inflorescence {zone}.

We see that an advantageous division of function is achieved in all these later stages of our series from the fact that as a rule, in the Araceae of these stages, when fertilization has taken place, all the gynoecia or pistils are found to have developed into fruits, while in the Araceae of stage I as a rule only a part of the many pistils form

fruits and in some cases, e.g. in *Anthurium brachygonatum*, which has a long spadix, and many others, it is always the case that only the basal gynoecia ripen {into fruit}. Here the division of function is less advanced {and} the scope for fertilization is greater. (see my paper: Über die Geschlechtsvertheilung und die Bestäubungsverhältnisse bei den Araceen, in this journal, Vol. IV, p.341).

The division of function in flowers is a widespread phenomenon; however, it is one of the most derived [am spätesten] phylogenetic processes and thus we see it occurring within the Araceae family in various Groups which have long been separated from one another and also in so many other families of Phanerogams in various Groups and genera as well as in the vascular Cryptogams and the Filicinae and Lycopodinae. The most advanced division of function in this direction, dioecy, is encountered in the Araceae only in the genus *Arisaema* in some species, e.g. *Arisaema ringens*. These relations [Verhältnisse] can also be considered from the standpoint that in the organism itself a struggle for existence takes place between different organs as regards their development. This is encouraged when repeated use occurs in the parents or the male and female protoplasm becomes concentrated in those regions which were previously always used in the ancestors [Die letztere wird da begünstigt, wo bei den Eltern wiederholt der Gebrauch erfolgte oder das männliche und das weibliche Protoplasma wird in derjenigen Region concentrirt, in der es bei den Vorfahren zuletzt immer Verwendung fand.]. Indeed, we often see staminodes develop around the gynoecia of the female inflorescence {zone}; but they no longer carry male protoplasm as do the true stamens; {the male protoplasm} only reaches normal development in the upper regions of the spadix. That {these} substances are separated {presumably Engler means here the separation of male and female protoplasm} is implied by the fact that we find bisexual flowers in so many androgynous inflorescences of the Araceae at the border between the male and female inflorescence {zones} but nowhere else. That the development series of the various Araceae flowers can be attributed to reduction I have already emphasized in my previous paper on the morphology of the Araceae (Bot. Zeit. 1876, p. 99) and in the introduction to my monograph (p. 24, 25) {i.e. the Mon. Phanerog. 1879} and I have also adhered to the sequence of stages suggested here in {proposing} the subfamilies or Groups [Unterfamilien oder Gruppen] of the Araceae which on the basis of the considerations I have previously expressed above (p. 147), I hold to be the {most?}

natural ones⁸. Other morphologists, particularly Eichler and Delpino⁹ ascribe great significance to reduction in floral development. However, it seems to me that it is just as advisable to treat it {i.e. reduction} “cum grano salis” {with a pinch of salt} for the clarification of floral forms as in the case of other phylogenetic development processes [phylogenetischer Entwicklungsvorgänge]; one should be on guard particularly against viewing simple development phases of a lower order, e.g. the flowers of Urticaceae, Betulaceae etc., as reduced forms of heterochlamydeous flowers. The reduction processes which we have touched on only in general terms and which we will later on elucidate more precisely, fall under Nägeli’s sixth phylogenetic law: “The parts of an ontogeny become unequal as functions which were earlier combined unfold and as new and different functions in the different parts are generated.”

8. The flowers

The individual flowers of the Araceae show many differences in the development of the individual flower units [Blütenformationen], apart from those already elucidated previously concerning sexual development, which can be brought into series, just as in the different developmental forms of the whole inflorescence. In general, apart from spiral or whorled arrangement, I hold the following {propositions} to be valid as regards the flower:-

1. The flower is a form of shoot which bears sexual organs [Sexualblätter]
2. The protection of the flowers is undertaken either by the subtending leaves of the individual floral shoots or by the shoot’s bracts situated nearest to the sexual organs.
3. The bracts of the shoot are either similar (homochlamydous; and then either bract-like (prophylloid) or petaloid) or dissimilar (heterochlamydous). If the whole floral envelope [Blütenhülle] is lost through abortion, then the flower becomes achlamydous; if one element {?whorl} of a heterochlamydous floral envelope is demonstrably lost {however}, it can be called monochlamydous.

⁸ I have made the same efforts to express the succession of stages in development in the family system in my treatments of the Rutaceae, Simarubaceae and Anacardiaceae; especially in the Monograph of Anacardiaceae it can be seen immediately from the whole arrangement the role that reduction has played in the progression of the family.

⁹ F. Delpino: Contribuzioni alla storia dello sviluppo del regno vegetale, Genova 1880, p. 33 ff. – Also compare my report on this topic in Bot. Jahrb. I, p.291.

4. If the sexual organs of a flower are different, then the stamens always precede the carpels.

5. The flower phyllomes [Die Blütenphyllome] of a unit can be limited in the number of their spiral cycles or whorls and where no constancy has yet been reached {in the number of} these spiral cycles and whorls, this limitation is also dependent on external factors (nutrition), just as the spiral cycles and whorls of cataphylls, foliage leaves and bracts in a leafy shoot with inconstant number are subject to variation.

6. In each unit, individual elements of the spiral cycles or whorls can be suppressed as a result of disuse or especially strong development of other elements. The influence of neighbouring flowers can make itself felt in this context.

7. The enlargement of the floral axis can have the result, though not necessarily so, that in the spaces occurring between larger phyllomes of the lower {floral} unit, two or more phyllomes of the following {floral} unit appear, while on the other hand as the floral axis becomes smaller in transverse section, only one element of the upper {floral} unit can form on two or more spaces of the lower {floral} unit.

8) The branching of the stamen phyllome [Staubblattphyllome] corresponds in the Angiosperms to the branching of foliage leaves; it is not necessary that the branches lie in a single plane.

Several of the above statements are not necessary for understanding the flowers of the Araceae; I want however use this opportunity to touch on some points of controversy and state my position in regard to them; in the following I give some explanation of the above-mentioned theses:-

Ad. 1. In recent times the {concept of} the pollen-forming “caulome” seems once again to have fallen into disuse, after it had been the fashion for a long time; on the other hand there are still many botanists who {consider that} the ovule or more frankly the seed bud {Samenknospe}, even within the same group of related taxa [innerhalb desselben Verwandtschaftskreises] spring out from the axis onto the leaf or from the leaf onto the axis. If one considers those families in which the position and number of ovules are variable, then one is persuaded that they {i.e. ovules} are parts of the carpel. We find this interpretation defended with great firmness in von Nägeli’s work (p. 512): “The ovules are phylogenetically derived from [die Fortsetzung der ...] the female sporogonia of the heterosporous vascular cryptogams, as the pollen sacs are derived from the male {sporogonia}. However, the sporogonia of vascular cryptogams arise from one or several superficial cells in various regions of the

sporophyll [des Sporenblattes] and thus have the nature of trichomes or emergences”. For von Nägeli there seems little value in the distinction between leptosporangia and endosporangia; moreover he would have ascribed to the ovules the significance of emergences, without further ado. One could also believe that Nägeli lays insufficient stress on the sporangia of *Selaginella*, but this is not the case, for he says on p. 477: “If the sporogonia in most *Selaginella* do not seem to arise from the leaf base as in *Lycopodium* but out of the stem just above the leaves, then I must regard them as situated on the leaf, for a part of the morphological leaf (in contrast to what is superficially discernible) is in any case inserted in the tissue of the stem, as I have earlier remarked and as is a consequence of the reduced leaves of *Psilotum*”. What is so little considered concerning the basal position of the ovules in the foundation of the ovary and yet the development history {Entwicklungsgeschichte} shows, is that some layers of ground tissue lying under the epidermis [Oberhaut] are often involved in the differentiation of the leaf; it is also clear that the leaves located at the end of the caulome will take up the whole apex with their bases alone and that the ovules situated at the base of these carpels, when they are single and orthotropous, must lie in the lengthening of the axis. Von Nägeli states on p. 512 the following on the ovules: “The descendants of the sporangia, the ovules, must have the same nature and be parts of the carpels. They could acquire a different meaning through apparent phylogenetic reduction, in that the carpel would diminish to a minimum and thus almost nothing but the ovule would remain (this is the case in *Taxus*, in my view), similar to the way that the male prothallus in higher vascular cryptogams dwindles almost to the antheridium. The ovule thus appears falsely in the guise of a phyllome. In the Primulaceae, if the central placenta was demonstrated to be a caulome apex, the ovules attached to it would be thus reduced carpels. However, I consider it more probable that the placentae are in all cases leaf parts and in the cited cases are formed at the base of the carpels. To explain the ovule as a caulom, or rather as a bud (seed bud) seems however to me phylogenetically unsustainable, since not a single one of the various ontogenetic relationships speaks even in some measure for this.”

Ad. 2. It is remarkable enough that in the whole family of Araceae the flowers lack {floral} bracts and so much the more that in some cases (*Orontium*) the inflorescence is divested rather early of the protection of the enclosing foliage leaves or of a spathe. It is quite inadmissible {however} to wish to seek in the dense arrangement of the flower the reason for the lack of the bracts. *Rohdea* and *Tupistra*,

which earlier authors sometimes mixed up with *Orontium*, have just as densely arranged flowers but in spite of this develop {floral} bracts; on the other hand, in *Pothos remotiflorus* the bracts are lacking just as is the other species {of this genus}. We must simply be satisfied with the recognition of the facts, that in all Araceae, {floral} bracts no longer exist. In the absence of prophylls the Araceae agree with very many Liliaceae. Whether they existed previously or not cannot be demonstrated. For hypothetical consideration of this question it may not be insignificant to consider the facts that the arrangement of the trimerous flowers of various Araceae is opposite. In most *Pothos*, in which I have studied the arrangement of the tepals [Perigonblätter] more exactly, e.g. in *Pothos Beccarianus*, the odd-numbered tepal of the outer whorl and the odd-numbered carpel are dorsal [stehen ... hinten], similarly in *Orontium aquaticum* and *Acorus calamus* in contrast both are always ventral [stehen ... nach vorn]. It is furthermore interesting that in *Spathiphyllum cochlearispathum* and *Sp. cannaeforme* the same parts are usually directed ventrally [nach vorn gerichtet], while in contrast flowers with the opposite orientation occur on the same spadix; also in *Cyrtosperma lasioides* some flowers show the inverse orientation in between normal flowers which have their odd-numbered carpels turned backwards. A rotation of the flowers by 60° to the right or the left can bring about the opposite pattern [entgegengesetzte Stellungsverhältniss]. Some flowers are also found here and there in these spadices with variable patterns which have a pattern intermediate to the two already described. One obviously thinks here of displacement by pressure. Since as will be shown later we repeatedly find such variation in {floral} patterns in male and female flowers separated from one another on the same spadix (*Synantherias*, *Spathicarpa*, *Mangonia*), together with variation in the number of {floral} elements, so I rather conclude that the position of the {floral} elements in these genera is no more fixed than their number. Very probably it is the absence of a floral bract that affects this situation, since it must always have an influence on the position of the following phyllome. On the other hand, in all floral envelopes of the Araceae which are constructed from two 2-membered whorls, the two outermost tepals [Perigonblätter] are lateral. The primitive [ursprüngliche] bract-like nature of the perigons [Blütenhüllen] is moreover quite evident in the Araceae.

Ad. 3. Here I have to remark that in agreement with most morphologists, I cannot quite concur with the view recently adopted by C. von Nägeli. He states on p.

509 of his Theory of Descent [Theorie der Abstammungslehre]: “However [im übrigen], the perigon essentially arose through adaptation (this one may readily acknowledge, Engler); on this account I would like to make it especially clear that one cannot regard as three phylogenetic stages {the series} 1. absence of perigon, 2. undifferentiated perigon, 3. perigon differentiated into calyx and corolla. These three forms are not genetically connected to one another in my view, since originally the stamens followed on from bracts, then the calyx or calycoid perigon arises from the upper bracts, the corolla or corolloid perigon from the lowermost stamens and forms intermediate between sepals and petals from transitions between bracts and stamens.”

For those who do not have confidence in von Nägeli’s epoch-making work, I would like to make a few remarks about it, which here come into consideration and should always, at any rate be heeded in morphology. On page 138 it is pointed out that the totality of the properties which we observe in organisms can be considered from two viewpoints [such unter zwei Gesichtspunkte bringen lassen]: 1. organization and division of function in general, 2. adaptation to the outer world. “Division of function in general runs parallel with organization and is a consequence of it; it brings about a three-dimensional separation of functions which had earlier been united and as a consequence a decomposition into partial functions. Adaptation to the outside world determines the particular form of the organization and the special nature of the division of functions and therewith the typical character and “Localton” {local appearance?} of the organism.” It is then further stated that the essential organization and the building up from raw beginnings are to be ascribed to internal causes, and to external causes the external decoration, to the former general matters, to the latter the particulars. The action of the external world is thus understood not in the Darwinian sense indirectly [auf dem Umwege] through competition and displacement, but rather as direct effects — displacement and with it the division of the lineage [der Stämme] come into consideration subsequently. Thereafter it is followed up on p.142 that the persistence of a stimulation over a long period of time, i.e. through many generations, also if it be weak and does not evoke any immediately perceptible reactions, nevertheless changes the idioplasm so much that heritable predispositions of noticeable strength are formed. We find also on p. 149 the following remark: “Stamens and petals are closely related to each other, the former transforming easily into the latter, a transformation which is visible in double flowers. The stamens are foliar organs, they appear in their simplest and most primitive form as small scale-like

leaves. The petals have arisen {presumably he means phylogenetically} from such scale-like stamens, {or} in some cases perhaps also from sterile bracts [Deckblättern] surrounding them {i.e. the stamens}, through considerably enhanced growth. This increase in growth may essentially have been caused by the stimulation which insects caused in their search for pollen and nectar by constant scrambling and small punctures {of the tissue}." I would like to disagree somewhat with this latter case; I am of the view that in most cases and not {merely} in some, the petals are derived from bracts surrounding the stamens; I {will} refer only to the *Liliaceae*, where we find, in the complete agreement of the {floral?} diagrammatic relationships, all possible stages between bract-like (prophylloid) development of the perigon and strongly marked corolloid (petaloid) development; here it cannot be thought that the petals have developed from stamens; furthermore, in the *Orchidaceae*, where we find bract-like development of both whorls, petaloid inner whorl and petaloid inner and outer whorls; and I recall {a similar state} still yet in the *Aristolochiaceae*, *Proteaceae* and *Loranthaceae*. With regard to the heterochlamydeous Dicotyledons von Nägeli's hypothesis is not so easily rebuffed, for here there is still the escape route that the sepals are to be interpreted merely as former bracts. In the *Ranunculaceae* it seems, even to me, not improbable that von Nägeli's view is correct. It is clear that the perianths of *Clematis*, *Anemone*, *Helleborus* and *Trollius* have arisen from bracts; however, the horn-like phyllomes that function as nectaries which in *Helleborus*, *Aquilegia*, and *Aconitum* follow the phyllomes usually designated as a calyx, can be regarded with just as much reason as staminodes, especially since in *Aquilegia* normal stamens are sometimes encountered in the place of the former structures. If, under this interpretation we could regard the *Ranunculaceae* as more uniform, we would have then in all of them a homochlamydeous perigon, either prophylloid or petaloid, and thus stamens and staminodes following after these. On the other hand it could also be asked why the bracts surrounding the stamens could not directly become nectar-secreting perianth segments [Blütenblättern] just as in *Fritillaria*. In certain cases perigon-like structures arise demonstrably from stamens and indeed in some *Araceae*, as will be shown later. The term perianth segment [Blütenblatt] would, if Nägeli's view for the heterochlamydeous Dicotyledons were generalized (it does not hold for Monocotyledons and homochlamydeous Dicotyledons), serve exclusively for the description [Bezeichnung] of the formation

[Ausbildung] of a leaf; the leaves designated with this name would be derived partly from bracts [Hochblättern] and partly from stamens.

Colourless (white) and thin or brightly coloured leaf structures also occur repeatedly in the Phanerogams other than immediately below the stamens, I remember for example the bracts of *Melampyrum* species, the involucre of the inflorescence of *Houttuynia* and *Anemiopsis*, and those of *Cornus suecica*, *Cornus florida* and other species, the coloured or white spathe of many Araceae, the petaloid nature of a large part of the sepals of *Mussaenda* and other Rubiaceae; here we have before us structures which differ from perianth segments [Blumenblättern] only by their position. Accordingly I am of the view that many plants (in part certainly under the influence of light) acquire the ability to produce pigments [Farbstoffe] at the end of their vegetative period which either in the region of the bract appears or first on the region of the stamens or yet first in the fruit; lack of colour is also produced under similar influences and to this is usually linked a greater development of the surface, as is observed in the green, morphologically equal foliar structures of the same or near-related plants. The preference by insects for the plants provided with such petaloid phyllomes has the result of maintaining them for longer periods. If we now could show in regard to the other properties, that plants modified in the previously stated ways agree with others which develop the same phyllomes in the same location but which still contain chlorophyll, then we are justified in interpreting the former as phylogenetically derived in comparison to the latter. However, it is necessary always to maintain the view that the petaloid formation of single or all bracts is a phylogenetic advance which occurs in later stages, that in addition petaloid homochlamydy does not need to be derived from heterochlamydy, but that sepaloid homochlamydy has existed as a previous stage both for petaloid homochlamydy and for heterochlamydy. Finally, monochlamydeous or achlamydeous flowers could arise from the same ancestral stage [Vorstadium] either directly by abortion or after petaloid homochlamydy or heterochlamydy have occurred. Although some Araceae still possess perianths in spite of a somewhat higher development of the spathe (*Spathiphyllum*, *Anthurium nymphaeifolium*), I nevertheless believe that it is the strong development of this bract, in which the pigments are accumulated, must have had an influence on the abortion of the perianth [Blütenhüllen], that to some extent the substances previously employed for the formation of the perianth have been sequestered by the spathe [von der Spatha vorweg genommen wurden]. As is evident,

naked flowers can thus be of various origins; they can as is highly probable in the case of the Cyperaceae, be naked from the first, but they can have become so also by reduction. A truly chlamydeous flower cannot arise from a completely naked flower of from one protected by its subtending leaf; this is only possible if the stamens become staminodes as a result of lack of use and as a consequence undergo a petaloid development. This is very probably the case in the Araceae *Staurostigma*, and simiolarly in *Dieffenbachia*.

Ad. 4. Many people will consider this proposition superfluous, since the similarity of all bisexual flowers in this respect seems to make it self-evident. However, in morphology there is much {to the contrary on this topic}, thus we find in J. von Hanstein's *Beiträgen zur allgemeinen Morphologie* on p. 44 the following passage: "The flowering spikes of these plants (*Arum*, *Calla*, *Richardia*) are undivided and the pistils and stamens arise laterally without the intervention of bracts, from the plastic cell tissues of the spadix, so that there is no delimitation of individual flowers. Both the individual organs and the entire spike could just as well be considered as a single flower, if one did not allow oneself to be guided by analogies with related, distinctly differentiated floral forms. With the omission, in such a way, not only of the division of the flowers but especially also the development of the shoot, and everything instead having merged into an almost completely undivided mass, thus one can speak finally neither of flowers nor of inflorescences, these structures having rather to be rated as indefinite intermediate forms nothing like anything else". A careful investigation of *Richardia* or *Zantedeschia*, of *Calla* and certainly of *Arum* would easily have been able to convince the author of this declaration that here the individual flowers are delimited, and it would have required only the investigation of *Dracunculus* or *Helicodiceros*, genera which are frequently assigned to *Arum*, to gain a more correct view of the matter. If one wishes to consider now the entire spadix as a single flower, which, as will further be discussed in the taxonomic part, would be the most completely opposite view possible, one would have in such a flower the pistils below and the stamens above, as in *Calla*, amongst others. If, however, one always finds the same sequence among those Phanerogams, of the most diverse construction, but in which both kinds of sexual organs occur in a single flower, then one has not the least justification to accept merely that an exception from the general rule has occurred, but rather one must investigate whether these phenomena, which others have interpreted as correct without further ado, do not



allow still another explanation which stands in agreement with the more general rules of development. In addition, the inflorescences of the genera cited by Hanstein are similar to very few flowers, while those of *Arisarum*, *Cryptocoryne*, *Pistia* are much more so, however here also the pistils or the single pistil lies below and the stamens or male flowers above.


Ad. 5. One need only consider in this regard how indeterminate is the number of carpels in for example *Myosurus*, *Adonis*, how changeable is the number of stamens in a single plant of *Helleborus*, or of stamen whorls in *Aquilegia* in order to find this proposition justified. We can see that nutrition has an influence on the increased or reduced development of stamen number in the fact that in *Agrimonia Eupatoria* sometimes only five stamens are produced and in other cases (in cultivation) up to 20¹⁰.

Ad. 6. The number of facts relevant to this question is known. In the Araceae however we encounter an extraordinarily large number of examples, which later will be discussed in more detail. Thus, for example, we find in *Homalomena rubescens* in the male inflorescence, 2-, 3-, 4- and 5-androus flowers next to one another as well as to flowers of the same number of stamens, in very different arrangements. Since we find, in Araceae which have undergone no reduction in their flowers, 4 or 6 stamens in two dimerous or trimerous whorls, so we have a basis to argue that 5-merous flowers in *Homalomena* are near to those of the ancestral form [Stammform]. Support for this assertion could be sought in the fact that the 3-merous flowers sometimes have the odd stamen positioned dorsally and sometimes ventrally [in relation to the subtending axis] and one could then argue that in the former case development of the outer whorl has taken place and in the latter of the inner. *Hydrosme Rivieri* is similar, at least in the lower part of the male inflorescence. In *Taccarum Warmingii* occur in the same inflorescence hermaphrodite flowers with 6 stamens and 6 carpels, then unisexuals with 6 free stamens and finally unisexuals with four connate stamens (see Taf. I, Fig. 13 – 15). The occurrence of 2- to 4-androus flowers, as well as female flowers with 2 – 4 carpels on the same spadix is so widespread in the naked-flowered Araceae that it would be excessive to enumerate all these cases here. In these naked flowers the stamens are all of such a thickness and the flowers are densely arranged, so that it is natural that the development of a greater number of stamens in one or

¹⁰ Göbel: Über die Anordnung der Staubblätter in einigen Blüten. – Bot. Zeitg. 1882, p. 353.

several flowers not only robs their neighbours of space but also substance {for their construction/formation}. Thus it comes about that we often find next to flowers with larger numbers {of sexual organs} flowers with fewer. Incidentally, I am not of the view that the position of the stamens within the flower of the Araceae is fixed. I have already pointed out earlier that we encounter differences of position in less densely arranged flowers. Furthermore one can well think, given the occurrence of trimerous

whorls with the arrangement  next to others with the arrangement , that here definite members of a 6-merous flower have developed; but this viewpoint cannot be easily reconciled with the occurrence next to them of 4-merous flowers

with the arrangement ; one would then have to accept that a shift in the ancestral arrangement happened, and one can overcome this difficulty with the explanation that because of the lack of the floral bract, the arrangement of the floral phyllomes is in general not fixed.

Ad. 7. This proposition refers to the relations which belong to the most difficult in floral morphology and thus most give rise to disputes. In the Araceae such cases do not occur. More than 6 stamens are only encountered in very few cases, particularly in *Typhonodorum*. {Cases of} More than 3 carpels are numerous, 4 to 3 somewhat frequent, in *Xanthosoma* and *Homalomena*, 5 in *Ophione*; several, even up to 14 in *Philodendron* Sect. *Meconostigma*. The number of cases in which with a larger number of carpels the stamens are also available is small; *Staurostigma* and *Taccarum* sometimes show 6 carpels in the spaces between 6 stamens or staminodes; otherwise in hermaphrodite flowers there are always half as many carpels as stamens; *Philodendron* with its often so numerous carpels is not closely related [verwantschaftlichen Beziehung] to *Staurostigma* or *Taccarum*; in my view the pleiomery of the carpels is merely an increase which is conditioned by the greater space of which here the individual floral primordia can take advantage on the large spadix.

Both the subfamily [Gruppe] to which *Staurostigma* and *Taccarum* belong, as well as that to which *Philodendron* belongs, are such that I must regard as derived due to their radically different anatomical relations [Verhältnisse]; in the subfamilies [Gruppen] which I am obliged to regard as representatives of an older Type I find

only a whorl equal in number to the stamen whorl. Certainly it is possible that in the anatomically more advanced subfamilies [Gruppe] the gynoeceium has maintained here and there a more primitive state [einer älteren Stufe]; however on the other hand I do not see why the phyllomes which cover the floral axis could not be produced in greater number given enough nutrient materials. This seems to me to be the case if the floral axis, which is expanded either in width or length, preserved enough room between the first stamen primordia and the apex and at the same time enough material is available for {the growth of} male sexual cells. Von Nägeli does not enter into these cases in greater detail; but it seems to follow from all of his deductions that he would contest such a hypothesis, which as is well known, is made very probably also through ontogeny [durch Entwicklungsgeschichte]. Von Nägeli only allows reduction a role merely in the reorganization of the flowers; for him (see p. 503) it is always the Type in which stamens and carpels are still present in an indefinite number of whorls which have developed from a still more primitive [älteren] {Type} with spiral arrangement; the Types with a constant number of whorls are the more derived ones [die späteren].

Ad. 8. This is not applicable to the Araceae; however I wanted to refer to it because von Nägeli (p. 509) considers branched stamens as the first evolutionary stage [Stufe] the, from which the unbranched ones are derived by reduction; no grounds are indicated {by him} but it seems to me that the polythecous stamens of the cycads and Cupressinae have been the reason for this hypothesis.

After these considerations, it is somewhat self-evident what are regarded as progressions [Progression] in the development of the floral parts in the Araceae.

Progressions of the floral envelope [Blütenhülle]

I. Stage. The leaves of the floral envelope stand in two separate whorls.

II. Stage. The leaves of the two whorls become connate into a single one and “fuse” {Engler’s quotation marks} with one another. – *Spathiphyllum cannaeforme* and *Sp. commutatum*, *Holochlamys*, *Stylochiton*, *Anadendron*.

Abortion of the floral envelope may occur in each of these stages, and also may happen before the bracts which precede the sexual leaves have associated into whorls.

Progressions of the stamens

I. Stage. The stamens stand in two whorls around the gynoeceium.

- II. Stage. The stamens assemble into a single whorl on abortion of the gynoecium. Quite often the space is still visible where the gynoecium would have stood (lower male flowers of *Hydrosme Rivieri*, *Taccarum Warmingii*), more often however the stamens stand close together in the middle {of the flower} so that thus the growth of the floral axis ceases earlier. Along with this is frequently associated a reduction in the {number of the} stamens to 5, 4, 3, 2. – *Homalomena*, *Philodendron*, *Dieffenbachia*, *Chamaecladon*, *Schismatoglottis*, *Arum*, *Montrichardia*.
- III. Stage. The stamens form a single whorl and their filaments are connate at the base. – *Dracunculus*, *Arisaema*, *Gorgonidium*.
- IV. Stage. The stamens form a single whorl and are connate throughout their length into a synandrium. – *Colocasia*, *Alocasia*, *Remusatia*, *Gonatanthus*, *Syngonium*, *Hapaline*, *Spathicarpa*, *Staurostigma*, *Taccarum*, etc. *Ariopsis* is a peculiar case where the stamens stand around an empty space and are laterally connate and these synandria are themselves all connate in a spadix.
- V. Stage. This stage can be derived noly from the second stage: the flower contains only a single stamen with dissimilar formation of the anthers. – *Biarum*, *Arisarum*.
- VI. Stage. The flower contains only a single stamen with shield-like formation of the anthers. – *Pistia*.

Progressions of the staminodes

- I. Stage. The staminodes of a female flower are complete and surround the gynoecium in equal number to the stamens in the male flowers. – *Staurostigma*, *Taccarum*, *Synandrospadix*, *Gorgonidium*, *Dieffenbachia*; sometimes also *Steudnera* and *Schismatoglottis*.
- II. Stage. The staminodes of a female flower are connate into a perigon-like structure. – *Staurostigma*.
- III. The staminodes of a female flower are only partly developed and partly suppressed. – *Spathicarpa*, *Steudnera*, *Schismatoglottis* sometimes.
- IV. The staminodes of a female flower are reduced to a single one of very definite location. – *Homalomena*.

However, the stamens of a male flower can also become staminodes and then we have the following stages:-

Stage Ia. The staminodes are free and stand around an empty space or are located close to one another. – *Schismatoglottis rupestris*, *Dieffenbachia*, *Philodendron*.

Stage IIa. The staminodes are associated together [mit einander consociirt] into a synandrodium. – *Colocasia*, *Remusatia*, *Alocasia*, *Typhonodorum*, etc. etc. Here it also often occurs that the synandrodes {become} connate and form the peripheral layer of the spadix appendix. – *Alocasia*, *Colocasia*, *Typhonodorum*.

Progressions of the gynoecium

I. Stage. The gynoecium is composed of two or more carpels and contains as many locules as there are carpels. The placentae are accordingly axile [centralwinkelständig].

- a. The placentae develop ovules throughout their length. – *Anubias*,
Chamaecladon, *Rhodospatha*, *Anepsias*, *Rhaphidophora*.
- b. The placentae develop ovules only in certain positions, at the apex, in the middle or at the base. – *Acorus*, *Zantedeschia*, *Anthurium*, *Stenospermation*, *Monstera*.
- c. Only a single ovule is developed in the middle or at the base of the locule. –
Plesmonium, *Amorphophallus pr.p.*, *Staurostigma*, *Taccarum*, *Dieffenbachia*,
Dracontium, *Pothos*.

These are in any case very late-occurring progressions; for we find them not only in closely related genera but also even in the same genus (*Philodendron*).

II. Stufe. The gynoecium is composed of two or more carpels and contains only one locule, since the margins of the carpels are only slightly turned inwards.

- a. The placentae are parietal and protrude rather deeply into {the locule}. –
Homalomena, *Xanthosoma*, *Caladium*.
Sometimes the carpel margins protrude so far inwards that the placentae seem almost axile.
- b. The placentae are completely parietal and protrude only slightly inwards. –
Schismatoglottis, *Bucephalandra*, *Ariopsis*, *Remusatia*, *Colocasia*.
- c. The placentae are found at the base of the ovary.
 - α. The placentae bear several ovules. – *Microcasia*, *Alocasia*, *Gonatanthus*,
Calla.
 - β. The placentae bear only 1 – 2 ovules. – *Typhonodorum*.

III. Stage. The gynoecium consists of two or more carpels, but these are developed very unequally, with only one locule fully formed, and the others more or less stunted. This case is not always demonstrable with certainty, but usually only implied by the number of stigma lobes and also sometimes by the position of the placenta. Not rarely one finds however (for example in the genera cited) traces of locules in individual gynoecia which demonstrate that there is not just a single carpel present.

- a. The parietal or (by development of a second locule or of other locules) axile placenta bears several or a few ovules. – *Cyrtosperma*.
- b. There is only one apical or basal ovule present. – *Lasia*, *Scindapsus*, *Culcasia*, *Syngonium*, *Hydrosme*, *Amorphophallus*, *Aglaonema*, *Anadendron*?

IV. Stage. The gynoecium is formed from a single median-positioned carpel.

- a. The placenta is parietal and basal, that is, it runs from the base to the apex of the ovary, or it is only basal and in both cases bears numerous ovules. – *Zomicarpa*, *Arum*, *Cryptocoryne*, *Pistia*, *Ambrosinia*, *Arisarum*.
- b. The placenta develops a few ovules either only at the apex or in the middle or at the base. – *Theriophonum*, *Sauromatum*, *Helicophyllum*, *Dracunculus*.
- c. The placenta develops only a single ovule at the base of the locule. – *Pinellia*, *Biarum*, *Typhonium*, *Anchomanes*, *Aglaonema*?

Finally, concerning the ovules themselves of the Araceae, we find all stages from orthotropous to hemianatropous, anatropous and amphitropous, and moreover with a long funicle or sessile, and thin, delicate, consisting of few cell layers, or thick and robust. This latter formation seems to be an adaptation phenomenon which is partly dependent on whether many or few ovules are developed. The development of the seed, which will be discussed more extensively later, is somewhat diverse, but here comparative ontogenetic studies are lacking, which encounter difficulties since relatively few species come into fruit in our glasshouses. In general, however, the dissimilarities seem also to be more adaptation phenomena; thus we find in different subfamilies [Abteilungen] that those seeds lacking endosperms with a stout enlarged embryo have only a thin membranous seed coat. Seeds with and without endosperm occur in individual subfamilies [Gruppen] which I must consider natural; the advance from seeds with endosperm to those without would thus be such that frequently it

occurs later, while in other plant groups it seems to have occurred earlier than the progression of other parts.

With this I will end this general overview of the [morphological] aspects occurring in the Araceae, and in the following sections I will show how within the individual major groups of the Araceae the genealogical connection{s} [verwandtschaftliche Zusammenhang] can be verified particularly from the floral structure. The sequence in which I present the individual subfamilies [Gruppen] has no significance in a phylogenetic sense [phylogenetischer Beziehung]; I begin with a group of related taxa [Verwandtschaftskreis] which I name the Lasioideae, on account of the fact that this group shows the most diverse forms of development of the inflorescence and so soon gives to the reader the opportunity to become familiar with the most important {morphological} phenomena [Erscheinungen] in the family Araceae.

9. Lasioideae

Among the large number of genera which R. Brown denoted as Orontieae and in the same manner were also artificially combined by Schott, we find some in which we cannot overlook a very far-reaching agreement; these are the genera *Cyrtosperma* Griff. (incl. *Lasimorpha* Schott), *Lasia* Lour., *Anaphyllum* Schott. Let us consider just these initially, although we will soon see that they are intimately connected to some others. The cited genera all possess a small, decumbent or crawling stem, more or less emergent above the soil, partly with elongated and partly with shortened internodes; but without a tuber. The rather long petioles and peduncles and also the rhizome and leaf ribs are provided with small prickles but in a manner which is highly variable among the different species, and I have no idea of their significance for the plant's life. If it should be thought that in *Lasia* these prickles are used for reinforcing the stem which climbs and sprawls on other plants, in other respects however the distribution of the prickles such that only a small part of them can serve as a means to help the stem become upright. The prickles perhaps act more as a means of protection from the attacks of certain animals. At any rate, the inconstancy of their occurrence shows their lesser physiological importance. All {these taxa} agree in possessing somewhat rigid leaves of which the first and simply sagittate, but the later ones frequently show a more extensive division of the blade, which is still also sagittate in

outline; thus pinnatifid and pinnatisect leaves occur in *Lasia* and *Anaphyllum*. We also find in all of them a spathe which is much longer than the inflorescence, and {the spathe} does not show a division a separation into tube and blade; in *Anaphyllum* and some species of *Cyrtosperma* the long upper part of the spathe is spirally twisted. The inflorescence itself is as simple as in *Acorus*; once the flowers are fully developed, then the lower part of the spathe, which is often widely opened while above it is still closed, provides entry for pollinating insects. Perigon and androecium are in most dimerous, but in some species of *Cyrtosperma* trimerous as in *Acorus*. Since in the same inflorescence of some Araceae both dimery and trimery occur together so one should give this little value. The gynoecium seems at first glance to be monomerous with parietal placentation in all taxa, although it to be observed that even in the same inflorescence (e.g. in *Cyrtosperma Afzelii*) the placenta is oriented in different directions (right, left). Recently I have found in spadices of *Cyrtosperma lasioides* and of *Lasia* next to unilocular ovaries, 2-locular ones with one fertile and one sterile locule. The placenta in *Cyrtosperma* is several-ovulate or bi-ovulate, in *Anaphyllum*, *Lasia* and *Podolasia* N.E. Brown uniovulate; the ovules are anatropous and show a tendency to amphitropy, the latter occurring also in *Cyrtosperma Afzelii*. The fruits have a rather non-juicy pericarp, which according to the number of ovules include one or few seeds, in which the endosperm has been completely consumed by the stout embryo. A great diversity in number of ovules and seeds occurs in the genus *Cyrtosperma*. The question may now be posed: do we have any justification to regard among these species some as belonging to a more ancient Type and others to a younger one? Furthermore, which of these two Types, the few-ovulate or the many-ovulate, is the older? Whenever we perceive in a plant and especially in an organism variability in an organ or in its number and position, we have justification to presume both that the present state is derived from another not so very long ago, and that from the present state another can appear, and that from similar Types having such variability others are derived. We find in the various gynoecia of an inflorescence of *Cyrtosperma senegalense* a change in the number and position of the ovules and similarly in *Cyrt. Afzelii* a change in the number and position of the seeds; in *Cyrtosperma senegalense* sometimes there is only a single parietal placenta with a few ovules on the side wall, and sometimes the placenta has many ovules and extends to the floor of the ovary. The number of seeds is here always less than that of the ovules since next to the ripe seeds, dead ovules occur. Has therefore, the many-ovuled

form, which bears the stamp of variability, emerged from a form which possessed many, perhaps more ovules, or has it emerged from a form which normally develops only few ovules, perhaps one a single one? Has reduction or addition taken place? Apart from multiplication, which occurs mainly through splitting, both {phenomena} are found in nature, addition especially frequently in monstrous structures. The decision as to whether addition or reduction has taken place lies essentially in the recognition of the physiological advantages which both evoke in the plant. If the number of ovules is greater, then there is the possibility of a richer development of seeds, thus apparently an advantage. However, we see in an extraordinary number of cases only a part of the ovules present in a gynoecium turning into seeds; nonetheless, the ovules are always developed in the same number in the progeny; for the presence of many ovules has the advantage that for pollination/fertilization [Befruchtung] more points of contact are present and the unfertilized ovules stop extracting nutrients from the plant. Let us compare for example the seeds in *Aesculus* or in *Castanea* which develop alone in a gynoecium with those which have arisen in 3's or 4's in the gynoecium. The former are twice or sometimes three times larger as the latter and the plants into which they develop much more robust and thus more resistant. The reduction in number of ovules in a gynoecium is thus always advantageous if the remaining ovules have a favourable position for the penetrating pollen tube. On these grounds I believe it justifiable to conclude that plant types with few-ovuled gynoecia either arose from those with the same number or from plant types with many-ovuled gynoecia, but that many-ovuled types did not emerge from those with few ovuled gynoecia. Of course, this concerns closely related plant types.

On the basis of this deduction I believe I am entitled to presume that the many-ovuled species of the genus *Cyrtosperma* stand nearer to the the original type and the few-ovuled species further from it by reduction; the genera *Lasia* and *Anaphyllum* represent a still further reduced type. However, I do not consider that these known forms of the reduced type are younger than the known forms of the more ancestral [ursprünglichen] type. On this we cannot have decision. The facts, however, that both many-ovuled species of *Cyrtosperma* occur in West Africa, the 2-ovuled ones in the Indian Archipelago and tropical America, the one-ovuled genera *Lasia* and *Anaphyllum* only in the East Indies, indicates that the many-ovuled type was more widely distributed and that from it, reduced types arose in different places.

Next to the above-cited genera there are however others, namely *Urospatha*, *Dracontium*, *Echidnium*, *Ophione*. In regard to the genus *Urospatha*, which has diversified in northern tropical Brazil and Guiana with several very closely related species, the leaves and inflorescences appear very similar to those of a *Cyrtosperma* or a *Lasia* with simple sagittate leaves; however, we note here the absence of the prickles; and also they have a rhizome, growing in swamps, which however is upright rather than horizontal. If now, on superficial consideration, the inflorescence seems to agree closely with those of the genera so far considered, a close inspection will reveal some important differences. Certainly, all the flowers are hermaphrodite; but the lower ones are smaller and sterile. This latter may have its explanation in the fact that here the spathe is tightly convolute at the base; however it is open above and {it seems} that the insects which visit the inflorescence disdain to visit the lower flowers hidden at the base of the funnel. The gynoecium, which is superficially similar to that of *Lasia* is here always 2-locular and in each locule bears below the middle two to more anatropous ovules, which are situated side-by-side on the axile placenta and not as in the pluri-ovulate *Cyrtosperma* above one another on a parietal placenta; also here the ovules are anatropous. Only one of the ovules in each locule ripens to a seed, or in general one per gynoecium, which as in the previously mentioned genera encloses an embryo which is not surrounded by endosperm. The completely isomerous flowers indicate a somewhat older type than the *Cyrtosperma* type. The fact that in *Cyrtosperma* the placentae of the individual gynoecia are situated either right or left and never above or below, and that furthermore sometimes both locules are developed and that both carpels in *Urospatha* are also located to the right and left, demonstrates, in association with the agreement in anatomical structure, nervation and floral structure their close relationship. The genus *Urospatha* very close to *Ophione* Schott; superficially they seem hardly different, as in *Urospatha*, the lower flowers are sterile; but the gynoecium is here not isomerous, but polymerous and 4 – 5 locular; each locule includes only a single anatropous axile ovule. It is frequently the case that a multiplication of carpels goes hand in hand with a reduction in the number of ovules; something similar happens in reproduction, so we have six ovules awaiting fertilization in the bicarpellate gynoecia of *Urospatha* and five in the pentacarpellate gynoecia of *Ophione*. I do not consider it justified to derive *Ophione* from *Urospatha*, [since] I would not wish under any circumstances to attribute the pleiomery of the gynoecium to *dédoublement*; I would only consider that without a doubt both genera

{have} a common origin, especially because the geographical range of the genus *Ophione* is adjacent to that of *Urospatha*. *Dracontium* is likewise found in tropical America. Here we have a rather different plant, but nevertheless there are unmistakably close connections to *Urospatha* and *Ophione*. The species of *Dracontium* suspend their above-ground growth for some time and in connection with this they have a rather different organization. The stem is completely subterranean and tuberous; after a number of cataphylls, a single robust leaf appears with a strongly warty or aculeate petiole and a tripartite and then cymosely further divided leaf blade, which usually agrees completely with the leaves of *Amorphophallus* and *Hydrosme*; the texture [Laub] of the leaf is thinner and more delicate, and hence the leaf is more short-lived. The large blade, spreading out in all directions, assimilates sufficiently during the few months of its existence so that the underground tuber not only to replace the carbohydrates that have been consumed, but also to multiply itself considerably. After a period of dormancy a few cataphylls appear and an inflorescence on a short peduncle, the spathe of which is kettle-shaped below while its upper part expands like a protective roof over the relatively short spadix covered only with bisexual flowers. The flowers are partly dimerous and partly trimerous, and the gynoecium is isomerous as in *Urospatha*; the locules are uniovulate as in *Ophione*. In contrast to the two last-mentioned genera, *Dracontium* is distinguished by a long style; the seeds are similar to those of *Cyrtosperma*.

A plant which was introduced by the expedition of Archduke Maximilian in Brazil occupies a peculiar intermediate position between *Urospatha* and *Dracontium*; it was superbly illustrated in the splendid work *Aroideae Maximilianae* in Plate 16 under the name *Urospatha desciscens* Schott. It is a swamp plant and develops several sagittate leaves together as in the species of *Urospatha* and also an inflorescence which however has a much shorter peduncle than is usual in *Urospatha*. The shape of the spathe is quite different from that of *Urospatha* species and is much more similar to that of *Dracontium*. The flowers are similar to those of *Dracontium*; the locules of the isomerous gynoecium each contain only a single basally inserted ovule {and} the style is indeed not so long as in *Dracontia* so far known, but in relation to the ovary is longer than in the *Urospathas*. Finally, as in *Dracontium* the seed has several corrugated longitudinal ridges. In these circumstances the plant cannot be assigned to *Urospatha*. To create a new genus, which would represent an intermediate between *Urospatha* and *Dracontium*, is awkward because the floral characters agree so much

with those of *Dracontium* and the Araceae genera are essentially grounded on flower and fruit characters. Hence I place this plant in *Dracontium* as a separate Section, which I call *Urospathopsis*.

Echidnium behaves biologically just like the umbrella-leaved Dracontia; it diverges essentially only by the gynoeceum which is formed of a single carpel and which encloses at the base of the ovary two ovules which, corresponding to their position at the base of the ovary, show no tendency to amphitropy. While the genera discussed hitherto are indisputably related to one another, the following genera appear to be somewhat more distantly so, but nevertheless find no better place with any other Araceae subfamily [Gruppe] than here. In tropical America we find the genus *Montrichardia*. Young plants have the appearance of young *Urospatha*; but then the plants acquire a considerably different habit because the internodes of the upright-growing stem elongate. Once the plant has developed to flowering, it branches sympodially, {producing} three other inflorescences after the first one. The reticulate venation of the leaves is similar to that of *Lasia*, *Cyrtosperma* and *Urospatha*; also we are reminded of *Lasia* and *Cyrtosperma* in one species, *M. arborescens* Schott by the prickly armature of the internodes and petioles. I have still not yet been able to ascertain the anatomical structure. A considerable difference is shown in the flowers; the lower third of the inflorescence is female, while the upper two thirds are male. There is no sign of a perigon or aborted stamens in the female flowers, nor of aborted gynoecea in the male ones. Thus there is here in the flowers themselves no evidence for a connection with the Araceae similar to *Lasia*; however there is also nothing which speaks against it. The gynoecea of the female flowers are unilocular, formed it seems from a single carpel and containing two basal, anatropous ovules. In *Echidnium* we have something similar. Finally the seeds lack endosperm, as in all the previously discussed genera; the thin integument is smooth as in *Urospatha*. In the male inflorescence the stamens are very closely packed but seemingly in a disorganized way; however, rather careful consideration shows that there are always three to five {stamens} per flower. The nature of the stamens speaks against a direct derivation from the genera so far discussed. While the other genera have a thin, broad filament, at the apex of which are situated the thecae, which are much shorter, adjacent and open with a slit, in *Montrichardia* there is no filament; the thecae open with pores and are separated from one another by an intermediate space and are situated almost on the dorsal side of the stamen, and they are overtopped by the thick, apically truncate

connective. However, the stamens are short and thick in almost all naked-flowered Araceae; this seems to be an organization [Einrichtung] which is correlated with the absence of a perigon in Araceae, which may be understood as follows, since the stamens become more robust as the result of suppression of this perigon so they can more easily manage without the protection of the perigon.

The relationship [verwandtschaftliche Beziehung] to *Cyrtosperma* and *Lasia* is stronger in certain African genera than in *Montrichardia*. The two West African genera *Nephtytis* Schott and *Oligogynium* Engl. have a crawling stem and sagittate leaves with venation which is very similar to that of *Cyrtosperma*; the inflorescence, borne on a long peduncle and with an eventually reflexed spathe has female flowers in the lower part and male flowers in the upper, without a perigon. The gynoecia contain only a single ovule, which in *Oligogynium* is situated at the base and in *Nephtytis* is at the upper end, and which develops into a seed without endosperm with a thin testa and very large embryo. The three to four stamens of the male flowers of *Oligogynium* also have relatively large anthers, but here they are not overtopped by the connective as in *Montrichardia* and at the base have a short, free filamentous portion. The still incompletely known genus *Cercestis* Schott, which is high-climbing and also occurs in West Africa, is closely related to *Nephtytis*. Finally, the genus *Rhektophyllum* described by N.E. Brown recently, also belongs to this group, as it shows very similar relations in the structure of the female and male flowers as *Oligogynium*, climbs high and has a similar formation to *Monstera* of perforations in the cordate-sagittate leaves; it should be remarked here incidentally that these {perforations} also appear in the above-mentioned *Dracontioides desciscens*. All these genera agree with one another in that at maturity the style is distinctly separated off from the ovary; I find the same characteristic [Erscheinung] in the same manner in the styles of *Hydrosme Hildebrandtii*; very probably this condition is more common in this subfamily [Gruppe]. We come now to *Anchomanes*.

As in all the Araceae discussed so far, the flowers reach to the end of the spadix. {We have here} also the young stages, the histological relations and the leaf venation which indicate relationship with the previously mentioned genera. The seeds, which emerge from a single, large basal ovule in a unilocular unicarpellate [monogynischen] ovary (in *Anchomanes Hookeri* as in *Lasia*, {the ovary} is covered with warts), are very similar to those of *Oligogynium* and *Nephtytis*; the first foliage leaves of the seedling, which follow the cataphylls, are sagittate and reticulately veined as in those

of *Lasia*, *Urospatha*, *Montrichardia*. Already we frequently find in the second leaf, a longitudinal slit between the anterior and one of the posterior segments, so that as in the leaves of *Dracontium desciscens* and *Rhektophyllum* {sic}, the following leaves are more like those of the latter genus in that now, on both sides, two splits reaching the margin appear and thus the leaf becomes pinnately partite. The following leaves show ever more far-reaching division and are double pinnatipartite, the individual segments broadly wedge-shaped and on the broad outer side with crescent-shaped lobing. On older leaves more or less numerous prickles occur. The stem remains underground and becomes a somewhat elongated tuber, from which springs later an inflorescence on a very prickly peduncle. The female flowers, formed from a median-situated carpel, show no sign of an aborted perigon or of staminodes, and the male flowers are similar to those of *Montrichardia*, {differing} only in that the anthers are completely lateral and not “dorsal”; {otherwise} the anthers are similar {to those of *Montrichardia*} in reaching to the base and being somewhat overtopped by the thick connective.

The genera *Plesmonium* and *Thomsonia* are joined to *Anchomanes*, but as parallel developments to *Anchomanes* and not to be regarded as derived {directly} from the latter. In *Plesmonium margaritifera* Schott the gynoecium is two- to three locular, in each locule with a single anatropous ovule that develops into a seed lacking endosperm; while in all the genera so far considered the funicle departs from the ovule in the middle or in the neighbourhood of the micropyle, but here we see the funicle arising at the basal end of the ovule, a behaviour which we find again in all the following genera except *Hydrosme*, which in the form of its ovule sides more with *Anchomanes*. Between the male and female inflorescence {zones} we find a number of sterile organs about the significance of which (whether aborted gynoecia or stamens) I cannot express an opinion without study of living material. The genus *Thomsonia* Wall. (*Pythonium* Schott) is more interesting and somewhat better known; here, fertile male flowers follow after the unilocular, uniovulate gynoecia and the stamens are grouped in threes and fives together; these groups {of stamens} are so densely crowded together, as is the case in most other naked-flowered male inflorescences of the Araceae, but rather separated from one another by a larger intervening space; they are situated on a short extension which thus represents the floral axis. Above the male inflorescence we find a more or less equally long “Appendix” [“Anhang oder Appendix”], covered with conical structures that are

somewhat larger than the fertile stamens. As I only know *Thomsonia* from illustrations I am not in a position to decide whether such a protuberance corresponds to a floral primordium in which the stamens have not become differentiated or whether it is a stamen primordium, in which pollen formation has been suppressed. We will later meet other cases where in this respect we will be able to give a definite decision; we must tentatively be content here to say that the appendix is not an axial structure corresponding to the peduncle in its tissue layers. Several genera remain still to discuss, which group around *Amorphophallus* and *Hydrosme* and biologically and in habit agree with *Dracontium*, *Anchomanes* and the two latter genera, with the difference that the so-called appendix above the male flowers is more or less smooth and for this reason can be regarded on a superficial examination even more easily as a simple axial structure.

The female flowers in these genera may be laxer or denser {but} always regularly arranged. The ovary may be three-, two- or only one-locular and has in each locule as in *Dracontium* one upright ovule at the base of the septum, although in *Synantherias* and *Plesmonium* it is situated in the centre of the septum. Since two- and three-locular ovaries occur in the same female inflorescence of *Amorphophallus campanulatus* and two- and one-locular ovaries in the same inflorescence in *Amorphophallus bulbifer*, {this character} has no value for delimiting genera. In unilocular ovaries traces are not rarely present that the gynoeceum is formed from two to three carpels, since sometimes a small empty locule is found next to those containing larger ovules.

In one genus, *Synantherias*, we find the male flowers delimited even more distinctly than in *Thomsonia*; four to five stamens form a ring around a space in which usually a gynoeceum would have plenty of room (cf. Plate I, Fig. 4) and are connate into a synandrium. Between the lowest male flowers and the uppermost female flowers we can see some protuberances with elongated rhombic bases; since these protuberances and the adjacent male flowers continue the parastichies formed by the female flowers, we must regard the former as certainly floral rudiments.

From the other genera we wish now to deal first with a plant which is more frequently cultivated and can therefore easily be further investigated by other botanists; this is *Hydrosme Rivieri* (Durieu) Engl. As indicated above, *Hydrosme* is distinguished from *Amorphophallus* essentially by the nature of the ovules. However, in *Amorphophallus Rivieri* Durieu, which Hooker fil. Illustrated in the Botanical

Magazine t. 6195 as *Proteinophallus Rivieri*, the ovules have the same structure as in *Hydrosme*; I have therefore assigned this plant also to *Hydrosme* (cf. Botan. Jahrb. I [1881] p. 187).

In the inflorescence of this plant one has the opportunity to obtain clarification on the nature of this type of inflorescence, which is so widespread in the Araceae family and is also formed in our *Arum maculatum*. While at first sight, the stamens of the male inflorescence appear to be quite chaotically arranged in comparison to the ovaries or female flowers, arranged in steep parastichies, on a closer examination, particularly at the border of the male and female inflorescences and at the border between the male inflorescence and the phallus-like “Appendix”, dispels any doubt that this confusion of stamens consists of many regularly arranged flowers.

We may examine next Fig. 1, drawn exactly from a live specimen. I have removed 5 pistils from this part of the inflorescence which lies at the boundary of the male and female inflorescences; it can be seen distinctly that each one is situated in a somewhat rhombic depression of the inflorescence axis and that the parastichies formed by the ovaries continue into the male inflorescence. This latter condition becomes even more obvious if the stamens are also removed; then one obtains the picture represented by Fig. 2. Here it is completely clear that the stamens are organized in groups and that these groups have a broader base than the individual pistils, but also that here the base has acquired an elongated form corresponding to the predominantly longitudinal growth of the spadix. The example shown in Figures A and B is especially interesting because at *c* there is a group consisting of an aborted gynoeceum and two stamens; in Fig. 2 it can be seen that the base of this group is of a size intermediate between the base of the ovary and that of the stamen group. In *a* and *b* we have groups of stamens between which there is a small empty space where thus it could be presumed that at the first stage of development a rudimentary gynoeceum similar to that in *c* would have developed but that its development was completely inhibited by the much stronger development of the stamens. The stamens in the other stamen groups are so densely crowded at the base that it may be presumed that the gynoeceal primordium, if actually present, was suppressed at the earliest stage. As is clear from our illustration, the stamen groups are 4 – 6 – merous; from their arrangement it is easily perceived that they belong to two whorls whose members alternate with one another; however some disarrangements and distortions of the typical arrangement are brought about by the marked elongation of the spadix. The

stamen groups can be removed by careful preparation in the whole male inflorescence in such a way as to clearly show their bases; one can then see with certainty that the male spadix is not covered with irregularly crowded stamens but that the latter belong to male flowers which follow the same rule in their arrangement as in the arrangement of the pistils, i.e. which is apparent in the female flowers.

This same inflorescence of *Hydrosme Rivieri* also shows very interesting and instructive phenomena [Verhältnisse] at the border of the male inflorescence and the so-called appendix, which are shown in Fig. 3 {of Plate I}. The groups numbered 1 – 8 are 4-staminate flowers with densely crowded stamens. In 9, 10 and 11 we see the stamens not quite covering the base of the flower, here a part of the floral axis or receptacle remains open as a result of the marked longitudinal growth which begins in this region. This is even more the case in flowers 12 – 19. In 12 we find there are still 3 stamens developed, but the fourth is no longer present, and thus there is a large space, in 13 we have a single fertile stamen, a staminode and a large space, similarly in 14, in 15 there are two fertile stamens [“Laubblätter” sic!], one atrophied one and a large space, where a lateral and median stamen would have developed, in 16, 17 and 18 we find still a fertile stamen and finally in 19 only a small staminode {remains}. Who would contest that the areas 21 – 27 are also the receptacles of flowers in which the stamens have not developed, {even though} their rhombic shapes are still more distorted than in the more basal flowers and that also with the exception of 26, clearly continue the parastichies of the flowers below them? Above these floral areas occur others which gradually merge their borders together, although here and there in the middle of the appendix indistinct and much more elongated rhombic floral areas can still be made out. These observations [Verhältnisse] thus show that the peripheral tissues of the “Appendix” are formed from floral primordia in which the male sexual organs have not developed, {and so} the “Appendix” is not simply the primary, flowerless main axis of the inflorescence. Histologically a strong difference can also be observed between this appendix and the inflorescence stalk {peduncle}. The ground tissue is permeated by much larger intercellular spaces than the peduncle, although the distribution and structure of the vascular bundles is otherwise the same. However while a ring of dense collenchyma strands is present at the periphery of the peduncle, this is not present in the appendix, but rather a more than 1 mm thick layer of thin-walled, starch-filled cells without intercellular spaces.

The tissue of the fertile stamens away from the thecae is of the same type. The whole outer layer of the appendix thus consists of the undifferentiated elongated primordia of male flowers.

Leaving aside the fact that in all organisms of a higher level we are obliged to presume their evolution from a lower level, the still only superficial fixation of the characters shows here that we have before us one type of construction [Bildung] which is derived from another. I may emphasize once more that bisexual [Zwitterblüten] flowers sometimes occur at the border of the male and female flowers, that the lowermost male flowers have a space between the stamens which in the bisexual flowers is occupied by the gynoecium, that in contrast the stamens of the male flowers above are densely crowded, that in the uppermost {male flowers} the stamens are placed once again more distantly from one another and gradually disappear. Should we presume that the ancestors of our plant had entirely unisexual flowers and then inflorescences with bisexual flowers evolved from these? This would be, physiologically speaking, a reversion since the already existing separation of male and female sexual organs is advantageous for fertilization. We also see that the gynoecium of the bisexual flowers is sterile; the plant gains no physiological use {from it}; in present-day conditions it makes no difference whether it develops or not, and indeed we often see that such bisexual flowers are quite absent. It is also important, as we shall see later in other subfamilies [Gruppen] of our family, that these bisexual flowers are situated at the border of the male and female flowers, and furthermore that it is here on the border where those male flowers are found in which there is still room for a gynoecium. These morphological facts indicate that the unisexual flowers have arisen from bisexual flowers by reduction and physiologically this is very understandable. It seems to me that the reason all unisexual-flowered spicate and racemose inflorescences have the female flowers at the base and the male flowers above can be explained as follows. Let us presume we have an inflorescence of bisexual flowers in the following arrangement:-

n n n
 m m m
 l l l
 k k k
 i i i
 h h h
 g g g
 f f f
 e e e
 d d d
 c c c
 b b b
 a a a

Let us further presume that the pollen emerges from the thecae and falls down, or as well, insects search the inflorescences downwards; the former case is true for very many Araceae. Let there be n whorls of flowers present and that the members of the following whorl alternate so that it is possible for the flowers of whorl a to receive pollen from $(n - 1)/2$ flowers (i.e. 6, if $n = 13$); in contrast c can receive only from $(n - 3)/2$ (i.e. 5) flowers, e from $(n - 5)/2$ (i.e. 4) flowers, and g $(n - 7)/2$ (i.e. 3). Thus the prospect for the flowers to be pollinated is greater the more basal they are situated, on the other hand the pollen is also more excessive the more basal the position of the flowers in which it germinates and certainly quite excessive in the flowers of the two lowest whorls a and b . The quite opposite situation occurs in the upper flowers, where here the prospect for the female organs to fulfil their function becomes lesser the higher is the whorl in which they are situated. If all the flowers of the basal whorls, let us say, up to whorl f , are always pollinated [befruchtet], the nutrients flowing towards them as a result of the development of these numerous incipient fruits will be completely consumed and these flowers will receive nutrients in preference to the gynoecia situated higher up {the spadix}. According to the law of heredity however, younger generations normally no longer develop the organs which in previous generations are not used repeatedly; and thus in the lower flowers the stamens fail to develop [wegbleiben] and in the upper flowers the carpels. It is evident

from these remarks that this reduction process must advance from the base towards the apex in the lower part of the inflorescence and in the upper part from apex towards the base, and it is also understandable that it is precisely in the zone between the now unisexual flowers, where flowers develop with both {types of} sexual organs or at least traces of the one sex alongside fully developed organs of the other sex.

In longer inflorescences which are covered with bisexual flowers to the apex, the flowering often proceeds rather slowly from base to apex. When the lower flowers attain fertilization [Befruchtung], the upper flowers are often at a much earlier stage and have no prospect of the development which fertilization would initiate while the nutrient stream [Saftstrom] flows in preference to the already ripening ovaries. In the first case the differentiation of the floral primordia is somewhat further advanced, and in the second less so, in some cases completely suppressed, even though the peripheral tissue layers of the inflorescence have the character of a developmental tissue [Bildungsgewebe]. It could also be possible that there is another cause involved in the development of the appendices which occur in so many Araceae, namely the rapid growth of these inflorescences. If I consider those Araceae in which “naked” appendices occur, it is evident that they are all {plants} in which the inflorescence is formed below ground and then, suddenly emerging from the ground enlarges greatly in a few days; it could be thought that the rapid growth of the inflorescence prevents the upper floral primordia from reaching full development. However there are strong arguments against this presumption. In the first place there are genera with underground tuberous stems and subterranean formation of the inflorescence in which the spadix is covered with flowers to the apex; secondly, one finds both in *Amorphophallus* as in our *Arum*, that the inflorescences formed below ground long before their appearance above ground, already show the same formation of the floral parts; already in September, and very probably also much earlier, we find, for example, in *Arum maculatum* that the pistils already formed with their ovules, the stamens with their thecae, the staminodes and the appendix, only everything much smaller than they later become, and the pollen and ova not yet quite ripened. The later rapid growth cannot thus be regarded as the cause of the suppression of floral development in the upper part of the inflorescence, so the cause lies in {their} non-utilization. The understanding of the conditions occurring in *Hydrosme* and *Amorphophallus* is made much easier by the fertilization of the genus *Pseudodracontium* N.E. Brown (Journ. of Botany 1882. p. 193 tab. 231), which I

myself have not been able to investigate as yet. One species of this genus, *Ps. Lacourii* Linden et André, was earlier described as *Amorphophallus*, because of the similarity in habit. Concerning the inflorescence, the gynoecia are here one-locular, with a single fat anatropous basal ovule, similar to that of *Hydrosme*; after the female inflorescence there follows a fertile male {inflorescence} which is twice as long as the sterile male {inflorescence} in the apical part. The male flowers are here separated from each other, as in *Synantherias* and consist of 3 to 5 cuneate stamens with distinct filaments. To judge by the illustration of *Ps. Anomalum*, the number of stamens is also here variable [is auch hier die Stellung bei Gleichzähligkeit der Blüten häufig wechselnd], and sometimes the stamens of a flower are partially connate with each other. The short appendix begins, separated from these male flowers by a truly naked portion {of the axis}, and is traversed by numerous deep furrows which delimit the individual flower rudiments. We will later frequently encounter such a formation of the appendix, particularly in *Alocasia*.

It will be perhaps possible for those who are not yet familiar with all the genera to understand that closer relationships exist between all the genera discussed here than between them and the genera to be dealt with later. Although one {group} has an underground tuber and the other a short aerial {stem} and yet others slender climbing stems, the nature of the laticifers [Milchröhren] is the same in {all} of them (although their distribution is sometimes a little different), the development of the embryo is very similar, the venation entirely similar, the leaf form in all its diversity in all cases {can be} derived from a sagittate leaf, as the latter also appear in the younger stages of all genera in which we have been able to make observations in this respect. I have earlier united these genera into a subfamily, the *Lasioideae*; I must still maintain this subfamily, even though in the *Genera plantarum* of Bentham and Hooker there is a different interpretation. Only in one respect is perhaps a change needed; I included in the *Lasioideae* the genera *Porphyrospatha* and *Syngonium*, which are more similar to the *Colocasioideae* in their anatomical characters [anatomischen Verhalten] and in their venation, but {more similar to} the *Lasioideae* in their embryological characters [embryologischen Verhalten]. I had, in favouring the latter, diminished the importance [zurückgestellt] of the anatomical characters; I believe however that this was not justified; for it can be shown that also in some other groups of Araceae there are forms with seeds lacking or possessing endosperm which are {nevertheless} closely related [nahe verwandt]. Of the remaining genera *Cyrtosperma*, *Lasia*,

Anaphyllum, *Urospatha*, *Ophione*, *Dracontium*, *Echidnium* form a closely related group in which however, there is a closer connection between the first three than between the last four; I have previously denoted all these as the *Lasieae*. I have united *Montrichardia*, *Cercestis*, *Nephtytis* (now *Oligogynium*, *Rhektiphyllum* {sic!} belong here) into a separate tribe, the *Montrichardieae*; this union is however somewhat unnatural, since *Montrichardia* is somewhat isolated by some exceptional [auffallende] characters, while the the others are closer to the *Lasieae* and indeed to the three first {genera} which I have denoted as the *Lasinae*. Concerning the genera which I have grouped together as the *Amorphophalleae* in the Suites au Prodr. p. 67, the genera *Anchomanes* and *Hydrosme* (here belong not only *Corynophallus* and *Proteinophallus* but also *Rhaphiophallus*) are much better linked to the *Lasieae* {by} the form of of their ovule, while *Plesmonium*, *Thomsonia*, *Amorphophallus* {and} *Synantherias* are similar in that the funicle emerges from the base of the ovule. These connections between the genera also show that if the groups were {instead} founded on the {characters} that in one case the inflorescence was covered with bisexual flowers, in another with unisexual flowers and in a third with unisexual and completely atrophied flowers, they would not be natural.

The relations of the genera to one another may be most easily surveyed in the following way {table follows}.

10. Aroideae

A pair of South American genera, *Staurostigma* and *Taccarum* remind us in some respects of certain *Lasioideae*. They have leaves with pinnatifid and bipinnatifid division, which are similar to *Dracontium*; there as here the branching is finally cymose. We will deal first with the genus *Staurostigma* which at the time when I wrote my monograph of the Araceae was not especially well known; the seeds in particular were insufficiently known. As a result there is a mistake in my monograph and in the Flora brasiliensis in regard to the seed which does not lack endosperm but is indeed albuminous and similar in many respects to the seeds of the genera adjacent to *Arum*.

We consider first *Staurostigma Luschnathianum*, of which plant very fine material in alcohol was provided to me by the favour of Herr Prof. Wittrock, collected by Regnell in Caldas in Minas Gerais. The leaves are sagittate in outline but the major segments [Abschnitte] are pinnatifid. The inflorescences, which have a rather long

peduncle, are somewhat connate dorsally with the spathe at the base; the flowers are in 6-membered whorls (Plate I, Fig. 5), to which are frequently juxtaposed a 5- or 4-membered one at the pointed tip of the spadix, approximately the lower third of the spadix bears female flowers and the upper two thirds male flowers. The gynoecium of the female flowers, which has deep longitudinal furrows, is formed from 3 – 6 carpels and is 3 – 6 –locular, the individual locules connecting to the stylar canal by means of a small opening at the base; the anatropous ovules, which have a short funicle, are usually horizontal, but sometimes upright and then turn their micropyle either towards the centre of the gynoecium or towards the walls (Fig. 7). As I had seen only few examples I had thought that it was normal for the micropyle to be turned towards the centre; but later I became convinced that the direction of the ovule is not constant. We find around the gynoecium an envelope which surrounds the ovary with a number of lobes equal to the stigmas. If one considers the form and development of this envelope one would be inclined to regard it morphologically as a perigon, as it physiologically completely corresponds to one. However, a comparison of these flowers with others of the same inflorescence leads to a completely different interpretation. In Fig. 7 a part of the inflorescence is projected horizontally; this is taken precisely from the border region of the male and female inflorescences. Of the four horizontal rows of flowers the two lower ones are purely female, and the upper purely male. The other three rows, as is visible from our figure, partly of flowers with the character of female flowers and partly of male flowers. What particularly concerns these latter are structures arising from the connation of 2 – 4 very broad stamens with fat connectives. The first flower on the left in the third row has a gynoecium with one developed stigma and one atrophied one; however, on the upper side of the envelope, thus precisely where the stigmas (and also the ovary) and no longer normally developed, there are 3 thecae; in the second flower of the same row we find 3 stigmas, the envelope without thecae and bearing red dots and dashes on the basal side, like the envelope of the lower flowers. The third flower is distinguished from the second because it has only two stigmas, but on the apical side there is a theca. In the fourth and fifth flowers we see no style and no stigma (the ovary is also atrophied to a great extent and without ovules); the envelope closes apocally more than in flowers 1 and 3 leaving only a small round opening; in both flowers we find four thecae on the side facing the spadix apex; in the sixth flower of the same row we can perceive a difference from the upper male flowers only in so far that we can here also see the

small round opening in the centre, which we saw in flowers 4 and 5 of the same row but which is lacking in the male flowers situated higher up. From the {structural} relations [Verhältnissen] here described it is clearly evident that 1) the flowers of the third row of our projection have maintained more or less the character of bisexual flowers, 2) the envelope of the female flowers is a staminodial structure, and 3) one cannot fail to appreciate also here, following the remarks made on the *Lasioideae*, that both the male and female flowers have arisen by reduction from bisexual flowers. In the same inflorescence available for this investigation one saw synandria at the apex of the spadix in which the development of the thecae was for the most part suppressed (cf. Fig. 6); the differentiation is finally suppressed right at the apex, and a small appendix is formed from the somewhat merged synandrodes.

Now that the significance of the envelope enclosing the gynoecium is clearly established by the intermediate forms between male and female flowers in *Staurostigma*, we can deal more rapidly with the related genera. In *Mangonia*, whose only species yet known, *M. Tweedianum* Schott has simple leaves, approximately the lowest fifth of the spadix is covered with female flowers; these are tri-gynous; alternating with the stigma lobes we find surrounding the gynoecium three broadly linear, apically broadened and somewhat thickened phyllomes which are doubtless staminodes. The number of ovary locules is here smaller than in *Staurostigma*, but there are 2 anatropous ovules in each locule, which are pendent from the upper part of the axile placenta. The part of the spadix above the female inflorescence is covered with scattered male flowers in its lower half, the stamens of which, connate by their filaments, form a somewhat stalked synandrium (the stalk is the product of the fusion of the filaments), on which the 4 – 5 stout, anthers are situated apically and are separate whereas in *Staurostigma* they were connate. The synandrodes which densely cover the upper part of the spadix, are distinguished from the synandria only by the fact that the parts corresponding to the anthers do not form pollen. In many respects *Mangonia* corresponds to an older Type than *Staurostigma*. *Synandrospadix vermitoxicus* Is very similar to *Mangonia Tweediana* in leaf shape. The spadix, which is mostly adnate dorsally to the spathe bears rather laxly arranged flowers, basally female, with a 3 – 5-gynous gynoecium and 3 – 5 triangular staminodes which by their development and structure could be mistaken for just so many tepals [Perigonblätter] (Fig. 10). The ovule of each locule is situated here near the base and is almost orthotropous since the funicle is unusually short, with the micropyle directed

upwards. On the border between the female and male inflorescences there are in my specimen bisexual flowers of two types, 1) fertile with normal gynoeceum and free stamens with triangular filaments (Fig. 9). In another flower higher up, the stamens are connate similar to *Mangonia* but with the difference that the stalk formed by the connate filaments is longer; the anthers however are overtopped by a slender style with an atrophied stigma, the rudiment of the gynoeceum which in this case does not develop (Fig. 11). We thus have here, as in *Amorphophallus Rivieri* and *Staurostigma Luschnathianum* evidence that the unisexual flowers of these plants and of other Araceae have arisen by reduction and can infer from this [daraus entnehmen] how little the division of the Araceae into those with bisexual flowers and those with unisexual flowers corresponds to Nature. The male flowers which make up the upper half of the spadix are synandria without any trace of a gynoeceum and which form an almost globose capitulum of 3 – 5 anthers (Fig. 12).

The genus *Gearum* N.E. Brown (Journal of Botany 1882, p. 196), is most closely related to *Synandrospadix* [in die nächste Nähe von ... gehört]. The structure of the gynoeceum is very similar, and the behaviour of the ovules almost the same. The author mentions in his short description that obovate organs are situated between the ovaries about the morphological significance of which he remains unclear; these are obviously staminodes, although they do not seem to occur correspondingly to the number of ovary locules in the same degree as in *Synandrospadix*. It is stated that there is a “staminodiferous portion” between the female and male flowers, but the staminodes are not described. The synandria are different from those of the previously discussed genus and agree more with those of *Staurostigma*.

Some interesting species belong to the the genus *Taccarum*, which shows a still greater degree of division in leaf development than *Staurostigma*. The most interesting species in *Taccarum Warmingianum*; for the inflorescence of the original specimen of this plant shows a great diversity of floral structure. The lowermost flowers are female, 5 – 6-gynous and have an equal number of stamens; adjacent to the uppermost female flowers there are a few bisexual flowers in which however the anthers tend to be atrophied (Plate I, Fig. 13). Then follow male flowers, the 6 – 8 rather stout stamens of which are separate and surround an empty space, which in the ancestors of this plant must have been occupied by the gynoeceum (Fig. 14). In the individual stamens, the anthers are developed distinctly below the apex. In the majority of male flowers the stamens are completely connate into a stout, cylindrical

body, which bears somewhat above the middle a continuous ring of anthers (Fig. 15). The other species are generally similar, except that in *T. peregrinum* (Schott) Engl. the synandrium is shorter and in *T. Weddellianum* much longer, and in the latter the ring of anthers occupies the uppermost part of the synandrium.

Still a further two genera lie adjacent to the five already mentioned, in which there is a highly distinctive arrangement of the flowers. While one of these genera, *Spathicarpa* is today cultivated in many botanic gardens, the other, *Spathantheum* is represented by only a few poor specimens in herbaria, and on this account have been published [herausgegeben] in my “Araceae exsiccatae et illustratae”. *Spathantheum Orbignyianum* Schott from the Bolivian cordillera first produces sagittate and then pinnatisect leaves; the inflorescence is adnate throughout its length with the spathe (Plate II, Fig. 16). At the base there are 6 – 8-gynous female flowers surrounded by linear staminodes; then however, there follows a region, up to above the middle of the inflorescence, in which 4 or 5 rows of flowers can be seen of which the two outermost are female, and the middle ones male, while the upper part of the inflorescence is taken up only with male flowers. The position and nature of the ovules is just as in *Synandropsadix*. The male flowers are synandria which recall those of *Taccarum Warmingianum*; however, while in the latter genus the anthers are overtopped by a cylindrical projection, here we find above {the anthers} a disc-shaped, deeply 5-lobed structure whose significance I will discuss in connection with the next genus.

The inflorescence of *Spathicarpa* has in recent times attracted more attention from other botanists since *S. sagittifolia* Schott has spread to rather more gardens. Whoever considers only developmental morphology [Entwicklungsgeschichte], could think that this expanded spadix, which bears flowers on one side, is thus an inflorescence with dorsi-ventral development. The comparison with other Araceae shows us however, that unquestionably we must regard the broadened structure which encloses the inflorescence as the spathe, adnate on one side to the inflorescence. That which occurs only partially in the genera *Staurostigma* and *Dieffenbachia* takes place to a greater degree here and in *Spathantheum*, in that the spadix is adnate throughout its length with the spathe. The arrangement of the flowers appears clearly in the young stages, is the upper, anther-bearing part of the synandria is cut away. (See Plate II, Fig. 17, 18, where a part of the inflorescence has been treated in this way). In the inflorescence shown in Fig. 18, 2-membered whorls of male flowers alternate from base to apex with 3-membered whorls which consist of a central male flower and two

lateral female flowers. In young inflorescences 5-membered parastichies stand out very distinctly to the right and left in which a female flower is situated at the basal and apical ends and three male flowers in the middle; I have already shown in the section dealing with the inflorescence (p. 155) how this inflorescence of *Spathicarpa* is related [in welchem Verhältniss zu ... steht] to that of *Staurostigma*. In the lower part of the inflorescence illustrated in Fig. 17 there is always a female flower next to a male one, either to the right or to the left; it seems at first sight that the flowers are in two orthostichies; if the synandria are cut away however, four orthostichies are clearly revealed as well as the alternation of the 3-membered whorls with the lower 2-membered ones, as is shown in the following diagram where a signifies male flowers and g female ones:

g	a	g
	a	a
g	a	g
	a	a
g	a	
	a	g
g	a	
	a	g
g	a	
	a	g

One can see that the division of the sexes which is found basally does not hold if one imagines the removal of one of the upper orthostichies. This makes it unlikely that the state shown in Fig. 17 has arisen from that shown in Fig. 18 by abortion, but rather that it is to be presumed that the smaller surface which the spadix offers for the development of flowers in Fig. 17 was the primary cause for the given arrangement of the flowers and that the sexual differentiation only followed subsequently; I further draw attention to the fact that male and female flowers are present in equal number in the lower part of the spadix, whereas in the upper part the male flowers are present in greater numbers.

In the male flowers (Synandria) {Engler's emphasis} the number and position of the stamens is variable; in the smaller part, shown in Fig. 19 we have 4-, 5- and 6-androus synandria. There are no facts supporting the supposition that a rudimentary

gynoecium is also included in the synandria. In *Synandrospadix* this was the case in certain flowers; in *Spathicarpa* I have not yet found {rudimentary gynoecia} although I have examined a considerable number of living examples. One can nevertheless doubt whether the lobed disc occurring above the anther-crown in the synandria is formed from the upper parts of the stamen, which in the case of *Taccarum Warmingianum* form the cylindric extension above the anthers, or whether this disc corresponds to the metamorphosed stigma lobes of the atrophied gynoecium. The former seems to me the more probable; a more certain conclusion cannot be reached in *Spathicarpa sagittifolia* since the thecae are so densely placed that one cannot decide which pairs represent an anther. In *Spathicarpa cornuta* (Schott Aroideae Maximiliana tab. 13) this is distinct more evident; the thecae belonging to a stamen are a little separated from one another, as is also the case in the free stamens of *Taccarum*; the connectives are horn-shaped and elongated over the thecae and bent outwards (Fig. 19a). It may be mentioned in passing that we find large stomata at the apex of the individual stamens of all *Spathicarpa*, through which the secretion of drops {of fluid} takes place.

In the female flowers, the ovary, which contains a single orthotropous ovule, is surrounded by 3 – 6 reniform or almost circular, basally truncate scale-like leaflets [Blättchen]; our illustration (Fig. 19) shows rather clearly that the number 6 is typical and that if fewer are present this is due to abortion caused by the pressure exerted by the young convolute [zusammengerollten] spathe and the sheath of the adjacent foliage leaf; for it is always the “leaflets” on the side of the female flowers facing the margin {of the inflorescence} which are lacking and never those on the side facing the centre {of the inflorescence}.

{The question} whether the “leaflets” surrounding the ovary are staminodes or perigonal structures cannot be decided by consideration of *Spathicarpa* alone, even if the fact that these “leaflets” have a large stomate at their apex as in the stamens seems to suggest {the former}. However the close connection to *Spathanthemum* and the other genera previously discussed leaves no doubt that these “leaflets” are staminodes and not perigonal structures. It still remains to mention a peculiarity of *Spathicarpa*. It can be seen from the illustrations in Fig. 20 – 22 that the part of inner integument which surrounds the micropyle is obliquely positioned; one can see also however that the oblique position is caused by a pendent lobe into which stylar canal extends. In this way the stylar canal opens well below the micropyle, while the absence of this

lobe would allow the penetrating pollen tubes to reach directly the micropyle. This lobe is probably to be regarded as the vestige of a septum which we find in the gynoecia of *Spathantheum* and *Synandrospadix* formed from several carpels.

Here an Araceae must be mentioned of which we possess nothing except a very remarkable inflorescence in the Leiden Herbarium; it is *Gorgonidium mirabile* Schott from New Guinea. A rather large boat-shaped spathe surrounds a 1½ decimeter long inflorescence, which bears in the basal part four somewhat distantly placed whorls of female flowers, while the whole remaining part is taken up with male flowers. The female flowers (Fig. 23) correspond to those of *Synandrospadix*, except that here the 4-locular ovary – in the locules of which the individual ovules have the same position as in the latter genus and in *Gearum* – is overtopped by a style more than three times as long, and the gynoecium is surrounded by 6 – 8 narrowly linear staminodes. In the male inflorescence the naked flowers are formed from highly peculiar stamens; these are similar to the filamentous staminodes and likewise very slender and long and end in three legs of which the two shorter lateral ones each bear a spherical, two-locular theca dehiscing by a pore (Fig. 24). In the lower part of the {male} inflorescence we usually find four of these peculiar stamens connate into a single flower; but with free filaments; in the central region the stamens of a flower are connate more-or-less with the lower parts of the filaments and in the upper region finally we find several of the filaments grouped into branched tree-like structures in such a way that it is no longer possible to say which belongs to an individual flower (Fig. 25). Unfortunately we know nothing more of this genus, which deserves attention because it replicates in a region so distant from South America as New Guinea, certain peculiarities in the structure of the ovary which we encounter otherwise only in South American genera.

A review of the Araceae which resemble some of the previously discussed Araceae in growth relations, leaf shape, venation and anatomy and which also have a perigon around the gynoecium, leads to the genus *Stylochiton* which developed in Central Africa and Natal with three species. This genus is interesting in a number of ways. We deal first with *Stylochiton natalensis* Schott from Natal (Plate II, Fig. 26).

The spathe which is above ground in this species, is completely closed in its lower part, only above the tube does the blade curl in laterally. The spadix is only a little longer than the spathe tube and is covered from base to apex with flowers, of which those in the lower half are female and those in the upper half purely male, {with} those on the border having rudimentary ovaries. Although we do not encounter

a perigon in any Araceae from the Aroideae subfamily, there is one present here; in the female flowers it is longer than the ovary, lying very closely to it and entirely enclosing it (Fig. 27 *a – e*). That this envelope is really a perigon and not something like a staminodial tube as we found in the individual flowers of *Staurostigma*, is made evident by the fact that we also find a perigon in the male flowers which is admittedly of a quite different shape; it is cup-shaped [schüsselförmig]. In the female flowers there is non visible trace of atrophied male organs. If the stamens are removed one can see that the male flowers are not at all very densely crowded and that the parastichies of the female flowers continue directly into those of the male flowers. However the {inference that} the unisexual flowers have here arisen by abortion from formerly bisexual flowers is here evidenced by the fact that flowers occur at the border of the two inflorescences with fertile stamens and a rudimentary gynoecium which has either a conical or shortly cylindrical shape; but there is no trace of ovule primordia (Fig. 28). It is remarkable that the stamen filaments are slender and thread-like, which is a very isolated phenomenon in the Araceae family. The 2 – 4-locular ovary has 2 anatropous, somewhat elongated ovules in each locule which are somewhat similar to those of *Mangonia* and like the latter attached at the centre of the placenta. The seed is rich in endosperm as in the previously discussed American genera, by which the axial embryo is surrounded. *Styl. hypogaeus* Lepr. and *Styl. lancifolius* have a very similar structure of the individual flowers and these two are similar in that the spathe is subterranean to a small extent and the closed tube is three times longer than the upper part which opens by a slit. The inflorescence is here as long as the whole spathe and the individual stamens have much shorter filaments than in *Stylochiton natalensis*. It is however very characteristic for these two species that there is a large space between the male and female inflorescences where not even atrophied flowers are found. Instead of several whorls of small female flowers we find here at the base of the spadix a single whorl of female flowers which are distinctly larger than those of *Stylochiton natalensis*, and moreover also differ in that each ovary locule holds several anatropous ovules. It follows from this information that the flowers of the genus *Stylochiton* come closer to perfect flowers than those of the previously mentioned American genera; for here we have a true perigon which we did not find in the latter and we have also flowers in which rudimentary pistils are developed next to fertile stamens; this shows that these flowers have arisen from perigoniate bisexual flowers which also represent an older Type through the fact that

the number of ovules in each locule is 2 or more. *Styl. hypogaeus* and *Styl. lancifolius* correspond to an older Type insofar as they have several ovules in their locules but on the other hand to a younger Type insofar as they have only a single whorl of few female flowers instead of many. However, the varied nature of these flowers can also have the consequence that the fewer flowers now present have much larger pistils than *Styl. natalensis* in which there is also more room for the development of more ovules than in the latter species, and also the consequence that the substance produced for the production of female sex cells is now divided between a smaller number of carpels. Be that as it may, the genus *Stylochiton*, to which no other genus is closely adjacent, represents the oldest Type among the genera discussed in this section, presupposes {the existence of}, in view of its structure, a still older Type which is as yet unknown. I do not know of any Araceae which are closely linked to any of those {so far} treated here; but there is a large number of closely related genera from the Northern Hemisphere, which are closer to this group than to any other. Also there is still yet one South American genus, *Scaphispatha*, of which only the inflorescence is known, which cannot well be placed anywhere else. Here we find completely naked gynoecea and naked male flowers in which usually 4 stamens are connate into a synandrium. The unilocular gynoeceum contains four anatropous ovules at the base which all turn their micropyle towards the corner which the funicle makes with the outer wall; on account of the position of the ovules, which all turn their dorsal side towards the centre of the ovary, it seems to me probable that the pistil is formed not from one carpel but from two or more.

We are led, by consideration of the ovary, from *Scaphispatha* to another South American genus *Zomicarpa*, which at the time when I worked on the Brazilian Araceae and the monograph {i.e. Engler 1879, Mon. Phan.} was very poorly known; however I placed it also in this subfamily. We find, in the “Aroideae Maximilianae” of Schott, which appeared later, three species were most excellently illustrated which were brought as living plants to Schönbrunn, but are now no longer alive. There is an unmistakable outward similarity with certain species of *Arisaema* in the shape of the spathe and leaves; but the unilocular ovary contains not orthotropous ovules but 6 – 12 anatropous ovules in the same orientation [Stellung] as in *Scaphispatha*. On ripening, the upper part of the funicle swells up in the same way as in *Arisaema* and many of the genera related to it. There are only few (3 – 5) female flowers; it is therefore very possible that the rather large number of ovules in each gynoeceum is

connected with this. The male flowers, which are immediately adjacent to the female flowers, are formed 2 -3, sometimes free or sometimes connate stamens which have short filaments and open apically by two pores. While in *Zomicarpa Pythonium* and *Z. Riedeliana* the male flowers are so densely placed that it is difficult to delimit them individually, in *Z. Steigeriana* they are more separated; here atrophy can also be detected as the upper flowers mostly contain only a single stamen; however then follows to the apex {a zone of} floral receptacles [Blütenanlagen] in which the stamens, each corresponding to a single flower, develop only into a conical filament, which merges into a cushion corresponding to the floral axis. The other two species do not show this but instead a smooth, club-shaped appendix follows immediately after the male flowers, almost the same as those of *Arum*; only in *Zomicarpa Riedeliana* a few little humps protrude from the appendix as somewhat more differentiated staminodes. The morphological significance of this appendix is naturally the same as in *Amorphophallus* and *Hydrosme*, genera which I have discussed previously in more detail. The recently proposed genus *Zomicarpella* N.E. Brown differs from *Zomicarpa* in that it has only a single basal anatropous ovule.

In all Araceae which are more or less connected to *Arum*, we find orthotropous ovules in the always unilocular ovary and in the berried fruits seeds with endosperm and an axile embryo. In almost all we find undeveloped organs between the male and female inflorescences which as we will see are mostly staminodes. Like the stamens, they seems sometimes to be arranged without any order, so that certain botanists who know no more of Araceae than a few species of *Arum* were induced to presume these to be inflorescences in which independent flowers had not yet been formed. Above the male inflorescence we also find staminodes in many species [Formen] but in the majority usually a smooth appendix.

We never find a trace of a perigon around the female flowers; Gasparrini and Polonio ¹¹ thought that they had been able to detect ontogenetically that a small four-lobed perigon was developed before the ovary, and which fused intimately with the later appearing ovary, so that the perigon was no longer detectable at maturity. However, Caruel ¹² showed that this observation was erroneous. The unilocular

¹¹ GASPARRINI: Osservazioni sull'esistenza dell'invoglio florale intorno ai carpelli dell'*Arum italicum*. Naepel 1851. – Translation in the *Annales des sciences naturelles* 3. sér. t. XV, p. 37. – POLONIO: Osservazioni organogeniche sui fioretti feminei dell'*Arum italicum*: Pavia 1862.

¹² CARUEL's reply in the *Annales des sciences naturelles* 3. sér. t. XVI (1852) and in *Atti della società italiana di scienze naturali di Milano* 1863.

ovaries of the Araceae to be discussed here are formed from a single carpel. We see this clearly first of all in *Arum* itself, where there is a parietal placenta covered to the base and to the apex of the locule with two rows of ovules and which always lies only on the side turned towards the spadix apex. In *Theriophonum* and *Helicodiceros* we find the ovules only at the upper and lower ends of the locule. In *Dracunculus* only at the upper end, and in *Helicophyllum* only at the lower end. In *Arisaema* and *Arisarum* the ovules are also basal, and in the latter genus covering the broad base of the ovary in such numbers that one could be in doubt whether the latter are formed only from a single carpel or from several; a few ovules are found at the base of the ovary also in *Sauromatum*, and only one in *Biarum*, *Pinellia* and *Typhonium*.

Atrophied female flowers are extremely rare. In some cases they seem to be present; but it is questionable whether we are dealing with atrophied female or male flowers. In *Arum* species, as in *A. maculatum*, *A. italicum*, *A. Dioscoridis*, *A. orientale*, we find that the parastichies [Schrägzeilen] of pistils continue into parastichies of individual or pairwise connate spherical bodies which end in a small or larger filament [Schwänchen]. These structures are frequently denoted as pistillodes; since however these parastichies run into the parastichies of the male flowers and above the male flowers the same structures appear but slightly smaller, there is no basis to necessarily consider as reduced female flowers these peculiar structures, which function partly to close off the kettle {spathe tube} that includes the female flowers; they could just as well be reduced male flowers or perhaps also reduced bisexual flowers. Sometimes male flowers are found in which a stamen is represented by a slender tail-like filament, and yet others in which we see two such filaments together; from this arises in consideration of these and other such cases the question whether the bulbous swollen part of the aborted flowers represents the floral axis or just the floral receptacle; we are consequently best advised to denote these structures simply as floral rudiments. These floral rudiments play a major role in the organization of the inflorescences of the Aroideae. Where they appear between male and female inflorescences it is usual for neighbouring female and male flowers to lie in the same parastichy; we also see that the floral rudiments lying next to and above the male inflorescence continue the parastichies of the male inflorescence; further up the regular arrangement is no longer recognizable on the one hand because in this region the differentiation of the flowers is partly or completely suppressed and partly because a distortion of the floral primordia [Anlage] results from the vigorous growth

of the upper end of the spadix. The distribution, number and form of these floral rudiments contributes much to the diversity which prevails in this subfamily [Gruppe]; these characters [Verhältnisse] frequently vary within the same genus and also within the same range of forms which we unite into a species; one can easily see that a spadix has a different appearance according to whether there are 1, 2 or 4 rows of such floral rudiments between male and female inflorescences, but it is also clear that the recognition as species of forms differing only in this regard has a very weak foundation. Cases where the spadix, normally almost entirely free of flowers, is covered with such floral rudiments are rather rare. One of the best known examples is *Helicodiceros muscivorus*. In *Helicophyllum crassifolium*, which is closely related to *Helicodiceros*, the whole appendix is covered with warts which are also to be regarded as floral rudiments, but only few appear. *Arisaema ornatum* Miq. (cf. Plate III, Fig. 29) is similar. It follows from the consideration of other species that each individual filament represents a rudimentary flower; in *Arisaema Steudelii* the male inflorescence ends with numerous filaments, which are completely connected by their position to the foregoing male flowers, {while} in *A. laminatum*, *A. Leschenaultii*, *A. concinnum*, *A. Cumingii* and others there is a zone of such floral rudiments adjacent to the female inflorescence and in such a position that the interpretation [Deutung] of each such structure as a floral rudiment is undisputed. At the same time it can be seen here that the unisexuality of the inflorescences, which occurs only in *Arisaema*, is the result of reduction. What I have previously said on the appendices of *Hydrosme* and *Amorphophallus* also applies to those of the genus *Arum* and its related taxa. These are to be interpreted neither as fully formed inflorescences nor as inflorescence axes; for the peripheral tissue of these appendices corresponds to the tissue of the stamens. If one sections for example the male inflorescence of *Arum Dracontium* so that one of the synandria, formed from three stamens, is cut, one can see on treatment with iodine that at the periphery only the contents of the stamen filament and the region of the {vascular} bundles within it turn blue, while the area between the flowers does not. On the other hand, in a section through any part of the appendix after treatment with iodine shows 3 – 4 cell layers at the periphery filled with starch {which is} the tissue for forming flowers that in some cases protrude as bumps but in other are completely suppressed. At the embryonic stage [in der Anlage] the stage of development [Verhältniss] of the appendix {in relation} to the inflorescence is sometimes the same as at maturity but in other cases quite different. So I find that in October in

subterranean inflorescences of *Arum maculatum* the relative development [Verhältniss] of the fertile and sterile inflorescence is the same as at maturity, but in contrast in *Pinellia tubifera* at the same period, instead of the appendix, which at maturity is many times longer than the male inflorescence, there is a small apical stub, hardly half as long as the embryonic male inflorescence, which already bears developed stamens. Here there is a much greater later growth of the appendix than in the other parts of the inflorescence. Very probably the same thing happens in the long, whip-like appendices of certain species of the closely related genus *Arisaema* (*A. speciosum*, *A. Griffithii*, *A. japonicum*).

As regards the male flowers, {their structure} is very easily understood wherever they occur distant from one another. An excellent example is *Arisaema Dracontium*, the inflorescence of which is illustrated in Plate III, Fig. 30. The spiral arrangement of the flowers can be seen at once, which is nowhere discontinuous, and it can furthermore be seen that each individual flower is formed from 2 – 3 stamens with connate filaments, and that further up here and there, as in *n*, a stamen is represented by an awl-shaped staminode, and yet further that sometimes, as in *m* and *o*, the flower consists of a single stamen. We find the much the same in the male flowers of all other species of *Arisaema*, differing only in that sometimes two stamens form a flower (*A. ringens*, *A. lobatum*), sometimes 3 (*A. atrorubens*, *A. filiforme*, *A. Schimperii* etc.), sometimes 4 (*A. speciosum*, *A. japonicum*).

These characters [Verhältnisse] are not so clear in other genera as in *Arisaema*. In *Dracunculus vulgaris* it is still easy to see that each 2 – 4 stamens belong to a particular flower, because here the rather long stamens are also partly connate. In Plate III, Fig. 31 half of a transverse section through the inflorescence is shown; next to it (Fig. 32) is illustrated some flowers from the upper part of the same inflorescence, which also show transitional structures [Übergangsglieder] from fertile to rudimentary flowers; here a tooth-shaped or awl-shaped structure corresponds still to each stamen; further up however a whole flower is represented by {one} such structure. Furthermore, I found that the arrangement of the rudimentary flowers was here no longer regular but much distorted. It is also fairly easy to see how many stamens belong to a flower in *Helicodiceros muscivorus* (Fig. 33, 34); but it is more difficult because the filaments are barely developed and the anthers are almost quadratic in transeverse section. The relationship of the individual stamens to each other becomes clearer if a thin tangential section is made of the inflorescence; then it

can be easily seen that every 3 – 4 stamens are oriented facing one another and form a single flower, and it can also be seen that here as in all cases considered previously, the fertile and sterile flowers are not irregularly disposed but are arranged in spirals. These relationships are difficult to see in *Arum maculatum* and its relatives. Here the stamens seem to be without order; at least at first sight, not possible to determine which belong to a flower; also in quite young inflorescences, which are formed in the summer, little more can be seen in the first flowers. If however the development [Stellung] of the stamens of the lower floral primordia is observed [verfolge ... aus], then it can soon be seen that every 2 – 4, usually 4 stamens together form a flower, and that those floral rudiments lying next to the fertile male inflorescence also bear protuberances, and in the floral rudiments a little higher up the two on the left have 1 or 2 stamens, while that on the right ends in a slender tail-like filament; still higher up there is also a pair of rather elongated flowers each with two stamens, but yet further up there appear 3- and 4-merous flowers. Furthermore it can be seen that the flowers illustrated here belong to 3 parastichies, denoted by *a*, *b* and *c*. *Helicophyllum* is similar to *Arum*. In *Sauromatum*, as is apparent from my illustration of a part of the inflorescence of *Saurom. venosum* in Fig. 37 of Plate III, one is easily able to discern that at least the lower flowers of the male inflorescence are each formed of 3 stamens and that the portion lying between the male and female inflorescences is covered with relatively few but notably elongated floral rudiments. (cf. also Fig. 36). In the genus *Typhonium*, which I believe to be closely related to *Sauromatum*, a regular pattern within the male inflorescence is hard to discern, while the female flowers, as in all other Aroideae are here in a perfectly spiral arrangement; however I have not succeeded in determining the spiral arrangement, at least in *Typhonium divaricatum* of which I was able to study a living plant, as in the genera previously; this seems to be more likely the case in the species of the Section *Heterostalis*; here it can also be seen that just like in *Sauromatum* the floral rudiments adjacent to the female inflorescence correspond more to male than to female flowers. The biologically very interesting genus *Cryptocoryne* presents few difficulties in the {interpretation of the} floral arrangement any more than does the very closely related genus *Lagenandra*; {*Cryptocoryne* has} an underwater inflorescence protected as if by a bell jar by down-folded lobes of the spathe which are partly adnate to its inner walls. In *Lag. Dalzielii* Schott and the other species the female flowers are spirally arranged and are followed by a few rudiments, then a rather longer, completely naked part of the inflorescence

axis and above this the male inflorescence, in which di-androus flowers are also spirally arranged. I was able to satisfy myself more completely of the state and arrangement of the flowers in *Cryptocoryne Huegelii* (see Plate III, Fig. 38). Here and in other species of this genus, instead of numerous spirally arranged female flowers there is only a whorl of much larger flowers containing more ovules. Since we sometimes see some sterile gynoecia inserted higher up alternating with the members of this whorl, it is hardly to be doubted that the genus *Cryptocoryne* represents a more reduced Type in comparison to *Lagenandra*; for the rest there are no other differences between the genera.

The male flowers of *Arisarum* are very interesting and easy to understand. We find in this genus as in *Arisaema* that the male flowers are somewhat distant from one another

But each male flower consists of a single stamen, as indeed also in *Arisaema Dracontium* and other species a single 1-androus male flower sometimes occurs among the 2- and 3-androus flowers. The single stamen here takes on a reniform, almost shield-shaped form in which the single anther bends around both sides and also away from the spadix axis. The monandry of the flowers in *Theriophonum crenatum* and *Ther. Wightii* is also well recognized, in which the individual stamens, as in *Arisarum* are distant from one another and are completely spirally arranged (cf. Plate III, Fig. 39). On the other hand, the male flowers of *Th. Dalzelii* (*Tapinocarpus Dalzelii* Schott) and *Th. Wightii* (*Calyptracoryne Wightii*), placed by me in the same genus, are composed of two stamens. We also find male flowers composed of a single flower in *Pinellia*, although here and there a flower formed of two connate stamens also occurs. It is not possible to detect spiral arrangement in the mature male inflorescence (cf. Plate IV, Fig. 43); however, in the early stage of the inflorescence formed in the summer, the parastichies formed by the individual stamens are rather distinct, from which it is thus evident that here also, each single stamen represents a flower. This situation however also allows another interpretation on which I wish now to remark. On the exposed [aufgerollten] inflorescence (Fig. 43) there are some structures denoted by *x* which have 6 pollen thecae, while the other quadratic ones nearby have 4. It is very possible that these are synandria, in which due to the complete connation of the ventral sides of the individual stamens have completely lost the thecae that were situated there. The flowers indicated by *x* would then be formed

from three stamens and the others each from two and the flower indicated by *l* would correspond to an incompletely developed stage.

The situation in the genus *Biarum* is very interesting; Schott's genus *Cyllenium* must be combined {with *Biarum*}, while the genus *Ischarum*, which I also reduced to *Biarum* perhaps is better separated from it. The typical structure [Verhalten] of *Biarum tenuifolium* and its numerous varieties is that shown in Fig. 42 of Plate IV. The inflorescence illustrated here is from a cultivated plant which agrees best with *B. tenuifolium* Schott var. *abbreviatum*; it is however difficult to delimit the individual forms, for the inflorescences differ not only in the young stage by the presence of a greater or lesser number of staminodes, but differences also arise later by the greater or lesser elongation of the floral rudiments and of the appendix which contribute to making the individual plants look very different. Our illustration corresponds well to the actual situation; it shows that the parastichies present in the female inflorescence continue unhindered into the fertile male inflorescence, although the development of the individual flowers is very diverse, particularly in the region of the lower floral rudiments; the regular arrangement only becomes somewhat distorted above the fertile male flowers. Otherwise it is remarkable how here orthostichies appear next to the parastichies so that we have here perhaps, as in *Staurostigma*, a whorled arrangement of the flowers. {But} this is inconclusive since the {appearance of the} primordia of the flowers takes place almost simultaneously. We see from this situation [Verhalten] that the male flowers consist only of a single stamen and that each of the sterile organs corresponds to a single monandrous flower; we also find here as in *Arisarum* the somewhat asymmetric stamens are oriented in the same way in all flowers. Whoever subscribes to the concept of pollen-forming caulomes could use *Biarum* and *Arisarum* as examples. The whole spadix could in the first place be interpreted as one flower composed of many alternating whorls, since the ovaries are formed from a single carpel. There is only the small obstacle in the way {of this interpretation} that normally in the flower the carpels follow after the stamens.

The species [Formen] which were recognized by Schott as *Ischarum* and *Leptopetion* are similar to *Biarum tenuifolium* in the structure of the female flowers. However, although the species [Formen] also delimited by Schott as a distinct genus *Cyllenium* are similar in the structure of the male flowers to [those of] *Biarum tenuifolium*, this is not the case in the taxon [Gruppe] *Ischarum*; here there are usually 2 – 3-androus flowers between which some monandrous ones (cf. Fig. 40); in the

various vicarious forms of *Biarum Bovei*, which occurs in Asia Minor, Algeria and Spain, the individual flowers are evident, especially those of the upper region of the male inflorescence { which are } sometimes more separated from each other (cf. Plate IV, Fig. 41). In *Biarum Olivieri* Blume, which is also known by the name *Leptopetion alexandrinum* Schott, 2-androus and 1-androus flowers are mixed together on the slender spadix, the upper ones also separated by larger intervening spaces. Accordingly, in the genus *Biarum*, or if one prefers, in the genera grouped around *Biarum*, the number of stamens in the male flowers varies from 1 to 3, so that it may be presumed that the forms with constantly monandrous flowers, like *Biarum tenuifolium* have arisen by reduction from { ancestors } like those still extant in *Ischarum*.

There now remains for us the well-known genus *Ambrosinia*, which in its leaf development and growth conditions shows itself to be related to subfamily Aroideae discussed here, but differs significantly in the arrangement of its flowers. Instead of a detailed description, I refer to the illustrations I have provided in Fig. 44 – 47. The single ventrally placed female flower shows great similarity to the individual flowers of *Cryptocoryne*, but is much larger; we find here a still greater number of orthotropous ovules which are attached at the base, as in *Cryptocoryne*; in *Ambrosinia* there is the least number of female flowers within the subfamily Aroideae but the flower has the highest number of ovules; we see that this single female flower occupies a large part of the space at the base of the ventral chamber. Since such a distribution of the flowers is found in no other Araceae but here, it is very probable that the expansion of the spadix axis and its adnation to the spathe walls is the first cause of the distribution, but also involved in this is the fact that at the time of pollination, the inflorescence has a horizontal position due to the reflexed spathe; the flowers which previously had probably developed on the side turned upwards were much less protected than the downward turned stamens, the pollen of which can be kept in the lower or dorsal chamber until the insects carry it away. The stamens, reduced to completely sessile anthers are usually 8 or 10 and are situated close together in two rows. Since each two anthers always lie opposite one another, it is doubtful whether they form a flower or whether each flower is represented by a single stamen.

If we look back once more at the numerous genera of this interesting subfamily of Araceae, we can see that even today there exists a homochlamydous form

(*Stylochiton*) and numerous achlamydous forms showing traces of bisexual flowers (the *Staurostigmatinae*), which can well be regarded as representatives of an older Type, particularly because the stamens and carpels occur in them in greater numbers; but even these forms are not linked by intermediates to the later mentioned genera, which are characterized by complete unisexuality of the flowers, a smaller number of stamens in the male flower (1 – 4) and monocarpidiate female flowers with always orthotropous ovules.

In the group of genera which stand more-or-less next to *Arum* and which we have therefore denoted the *Arinae*, we can easily construct two series according to the development of the flowers, the one with consideration of the number and position of the ovules in the consistently monocarpidiate gynoecia and the other with consideration of the androecium; it is seen immediately that the two series are not congruent, that many genera which are similar in the structure of the androecium show differences in the gynoecium. These differences, such as basal ovules, tholifixed ovules, parietal ovules, single or numerous ovules, are very often found in genera which are so closely related that without observing the gynoecium we would place in the same genus. For this reason it may seem better to put more weight on the differences in the male flowers which mainly concern whether the flowers are monandrous or 3 – 4-androus. Must we therefore presume that the monandrous flowers have arisen from tri- or tetrandrous ones by reduction? Or is the contrary more probable, that the tri-androus ones etc. originated by addition? Or, finally, is it more probable that both Types originated together? Ontogeny [Entwicklungsgeschichte] can explain nothing in this case, even if one could see more than what it actually possible to see. For example, were we to find in the flowers of *Arisarum* a rudiment of a second stamen next to a fertile one, this could just as well indicate the initiation of an addition as of a reduction. Physiologically it make no difference whether the densely packed stamens belong 3 – 4 to a flower as in *Arum* and *Helicodiceros* or whether each stamen corresponds to a single flower; for reproduction the only thing that matters is the mass of pollen produced and the positional relations of the male inflorescence to the female one; in fact the space taken up by the thecae of the monandrous stamens of *Arisarum* or *Pinellia* is not much less than that which those of the 2- and 3-androus flowers of *Arisaema* occupy. It is hence incomprehensible why species [Formen] with 2- and 3-androus flowers would develop from those with monandrous flowers, while it is certainly comprehensible

that wherever the centre of a flower is not occupied by a gynoecium or the rudiment of one, in place of 2 – 4 staminal initials a single one will develop, in which all the nutrients for the male sexual cells will be used. It is natural that several stamens are developed peripherally if the apex of the floral shoot is still undergoing active growth and has yet to produce other foliar structures (the carpels); however as soon as the abortion of the gynoecium gives cause for a lesser activity of the apex, the stamens become more closely adjacent to one another and they may become connate (as in *Arisaema*) or only one stamen develops in their place, which is of course no more sharply differentiated from the tissue of the floral axis than a laterally positioned stamen whose origin also does not lie in the plane formed by the axial surface. Otherwise, the anthers are asymmetrically triangular [ungleichseitig] both in *Arisarum* and *Biarum*, from which it may be concluded that here the stamen is not yet completely terminal, while in *Pinellia* the stamen is developed symmetrically (provided that here we are not dealing with two connate stamens).

The above consideration showed that the transformation of monandrous flowers into 2 – 4-androus ones would have no physiological advantage, while on the other hand the transformation of 2 – 4-androus ones into monandrous flowers requires less work from the plant and is a simplification which brings no disadvantage to the species so long as the pollen produced is used to good purpose. Solely on these grounds, and not on the basis of ontogeny [Entwicklungsgeschichte], we are justified in regarding the monandrous forms as the reduced ones and also the advanced ones. Now we can also see the beginnings of such a reduction in the monandrous flowers which sometimes occur in *Arisaema* species (e.g. in our illustration of *A. Dracontium* on Plate III, Fig. 30), and also the flowers of *Dracunculus vulgaris* (cf. Plate III, Fig. 32) which have only one fertile stamen and two sterile ones. Otherwise, the genera with monandrous flowers are only partly related in such a way to the genera with 3 – 4-androus flowers that a derivation from the latter could be presumed. *Pinellia* stands in this relation to *Arisaema*. The latter genus also to be regarded as ancient on account of its wide distribution in a large part of the northern extratropical region, in the mountains of Abyssinia, East Indies, China and Java, while the genus *Pinellia*, restricted to a part of East Asia [Ostindiens] (northern China and Japan) has more the character of a younger, locally evolved {taxon}. I have already indicated previously that *Typhonium* seems to be closely connected to *Sauromatum*. *Biarum* should be linked most closely to *Helicophyllum* through *Ischarum*. In contrast it seems to me

that at first sight a close link between *Arisarum* and any one of the other genera cannot be determined.

We have, in the first place, no support for the descent of the *Arinae* from a Type with bisexual flowers in intermediate taxa. In this respect there is a gap between the *Stylochitoninae* and *Arinae* as between the *Staurostigmatinae* and *Arinae*; however on the other hand these groups are so close that their common origin is not unlikely, particularly as the distribution ranges of both complement [sich ... anschliessen] that of the *Arinae*. A summary of the structural relations of the flowers of this series of related taxa [Verwandtschaftsreihe] is provided in the following table and indeed in a way that the phylogenetic connections between the genera can be discerned.

{Table follows}

11. Pistioideae

As I have previously shown, the genus *Pistia* is connected rather closely to *Cryptocoryne* as regards its shoot organization, despite its externally remarkable appearance (see my treatment in *Nova Acta l.c.* p. 104, Plate 5) and the construction of the real sympodium is no different from that of a flowering *Philodendron*. The structure of the inflorescence is also completely explained by the structural phenomena of other Araceae, especially of certain Aroideae. We find, in the small spathes which terminate the individual shoots of the sympodium, a small inflorescence axis adnate to the base of the spathe, which bears an single gynoecium standing opposite the spathe, as in *Ambrosinia*, this is the only female flower (see Plate IV, Fig. 48, 49).

Here there are also, as in *Ambrosinia* and *Cryptocoryne*, numerous ovules on the entire basal surface of the ovary. In the area where the style terminates, we find two peculiar excrescences of the inflorescence axis, one roof-shaped, which at first covers the stigma but later becomes overtopped by the upper end of the style, and then a funnel-shaped one, on which the pollen from the more highly situated anthers collects (Plate IV, Fig. 49). These excrescences are on the one hand comparable with the spathe walls of *Ambrosinia*, and it is also on the other hand possible that they are formed by the connation of staminodia; definite evidence for the latter view is however, lacking. Around the end of the spadix there are sometimes 4 sometimes 5 – 8 shield-like stamens in a whorl (Fig. 50, 51). It follows from this that we must regard each individual stamen as a single flower; and we thus have here, as in

Arisarum, flowers of both sexes reduced to the smallest degree possible, i.e. to either one stamen or one carpel.

Apart from the adaptations represented by the peculiar mode of growth of the *Pistieae*, it will be found that these plants show no peculiarity which cannot be found also to a certain degree in the *Aroideae*. Only anatomically do they differ by the lack of laticifers [Milchsaftschläuche].

Adjacent to the *Pistioideae* lie the *Lemnoideae*, the vegetative organs of which are modified in a different way but the floral arrangement of which permits without difficulty a derivation from the situation predominating in the *Aroideae* and *Pistioideae*. However it is rather the nature of the seed and the behaviour of the embryo at germination which impels us to place the *Lemnoideae* next to the *Pistioideae*.

The other structural relations [Verhältnisse] do not provide support for this placement; for the more a form is reduced the greater is the number of forms from which it can be derived, and thus it is especially the plant groups with reduced flowers and shoots which are most difficult to place within the system. I have gone into greater detail concerning the links between *Lemnoideae* and *Pistioideae* in my treatment *Vergl. Untersuchungen* etc. p. 215 – 219 (59 – 63).

12. Philodendroideae

The genera grouped together by me as the *Philodendroideae* are similar in having regularly arranged laticifers [Milchröhren], as in the *Aroideae* and most of the *Lasioideae* {NOTE THIS!}, and in that in the leaves the lateral veins of different orders run closely parallel to one another, more so than in any other subfamily [Gruppe] of the *Araceae*, and finally in that the embryo is surrounded by an abundant endosperm. The flowers are always unisexual and almost always naked, although we can detect staminodes next to the ovaries of individual flowers in several genera and thus presume with justification that the unisexual flowers have arisen from reduction, particularly as these have similar positional relationships as in the other subfamilies in which reduction occurs.

As a starting point for the investigation I choose *Schismatoglottis rupestris* Zoll. et Mor., of which I have illustrated the central part of the inflorescence in Plate V, Fig. 58. The inflorescence axis in this species and in others is of very different

thickness in the different zones, in the zone of the female inflorescence it becomes thinner from the base upwards, then follows an almost cylindrical {zone} covered only with a few stunted flowers, and thereafter a clavate portion which becomes thinner both towards the base and the apex, and which in its lower half bears fertile stamens and in its upper half staminodia. As a result of the fact that the spadix is now thinner and now thicker, the arrangement of the flowers is not quite regular, particularly not in the upper part of the spadix. The female flowers are spirally arranged; between them however we see appearing here and there peculiar linear organs with their apices ending in a white, globose head, and which, as will be shown, are staminodes. At the base of the female inflorescence these structures are found in greater numbers, often standing 2 – 3 per ovary. At the upper limit of the female inflorescence, however, there are female flowers situated more distantly from one another, around whose gynoecea we encounter 2 – 3 of these structures. A little higher up, 3 -4 of them are situated around a space in which a gynoeceum would have been located, and still higher up more-or-less within the male inflorescence we find several examples of {flowers with} two of these structures together with a fertile stamen, until finally flowers formed entirely of 2 – 4 stamens follow. The uppermost part of the spadix finally is again covered with staminodes but which in this zone have a different morphology [Ausbildung] to those previously mentioned. In the ovaries we find two or three parietal placentae bearing in two rows hemianatropous or sometimes orthotropous ovules on a long funicle. Since in the individual species of *Schismatoglottis* a great variation occurs in relation to the staminodes occurring in the female inflorescence, so it cannot disconcert us that in some species they are entirely absent. This is also the case in the genera *Bucephalandra*, *Piptospatha*, and *Rhynchophyle*, which are closely related to *Schismatoglottis*. On the other hand in the genus *Microcasia*, which is characterized by basal ovules, in contrast to the former genera which have parietal ovules, we find between the female and fertile male inflorescences a zone covered with staminodes that are different from those of the upper zone. Since only sparse dried material was available to me for this purpose, I could not determine whether perhaps a grouping by number and position of these {staminodes} was recognizable.

The genera *Homalomena* and *Chamaecladon*, also related to *Schismatoglottis*, are found in the same geographical region in which the previously mentioned genera occur, namely the Indo-Malayan region. *Homalomena rubescens* is found in most

botanic gardens, so that the possibility of future investigations is easily provided; on this account I will discuss this genus in rather more detail.

The male flowers of each inflorescence clearly reveal the inconstancy of the numerical relations {of the flower parts}; we find on almost every square centimeter of the male inflorescence 2-, 3-, 4-, 5-androus flowers. Thus it is as well to note that in regard to the arrangement of the stamens, there is no other regularity to be recognized than that there are always 3 – 5 stamens with extrorse anthers tightly crowded together around a central point. In trimerous flowers the arrangement of the stamens varies in such a way that the odd stamen is sometimes situated basally {in the sense of the spadix axis} and sometimes apically, although the former case is by far the most predominant. In tetramerous flowers the stamens, when viewed from above, appear as if they belonged to a single four-membered whorl; in other cases the surface appearance is such that two stamens stand to the exterior and the two others are partly enclosed by the former; however here the seemingly exterior ones {stamens} can be either lateral or median. Frequently, arrangements intermediate between those just described can also be observed. Even sections made closely at the base of the stamens show complete whorls in many tetramerous flowers, but in many cases also two 2-membered whorls; it is probable that the oblique configurations are caused by the mutual pressure of the flowers which must have an effect from their first appearance onwards. The division into two two-membered whorls comes about through the fact that either both lateral stamens or both median stamens grow somewhat more strongly and thus interpenetrating, push out the other two to some degree [... etwas stärker wachsen und dadurch gegen einander dringend die beiden andern etwas herausdrängen]; the commonest case is the stronger growth of the two lateral stamens. Male flowers with 5 stamens and 2 stamens are rarer than trimerous or tetramerous ones, but nevertheless are found on nearly every spadix. If the flowers are removed from the spadix by cutting immediately at their bases, one can distinctly see narrow gaps between the basal parts of the individual flowers. Most of the positional relations of the male flowers of *Homalomena* discussed above are explained in Fig. 52, which shows only a small part of an inflorescence after nature [nach der Natur {= ?from a living specimen?}]

One finds sterile male flowers at the border of the male and female inflorescences in somewhat lesser number. Fig. 53 shows a small part of the border zone between male and female inflorescences, that is very instructive. At first sight

there is no regular arrangement to be seen, but on closer inspection one soon sees that which fertile male flowers show, particularly in transverse sections; one recognizes here also that the stamens (lacking pollen) are not irregularly thrown together but that each 2 – 4 belong to one flower; in the figures the staminodes belonging to a flower are denoted in the same way as the stamens belonging to a fertile flower. As regards their development, the gradual transition from a normal stamen to a clavate staminode is easily seen; and in particular there remains no doubt about the fact that the structures standing in front of each ovary are morphologically completely equivalent to the staminodes of the sterile male flowers. In spite of numerous attempts I have been unable to find in the transition region between male and female inflorescences female flowers with more than one staminode.

The female flowers abut the male inflorescence without any interruption; if the stamens and staminodes of the transition region are cut off, one sees the oblique lines of the female flowers continue into those of the male flowers. As in the male inflorescence, here also trimerous and tetramerous flowers alternate, and also displacements occur so that the ovary locules are not always oriented in the same way. The gynoecia of the lowermost female flowers are considerably larger than those further up. As regards the thread-like, thickly clavate-tipped structures between the gynoecia, I have already previously denoted these as staminodes. That they are such, is easily demonstrated. The structures could be : 1) stunted gynoecia, they could thus correspond to an atrophied female flower; 2) rudiments of a perigon; 3) staminodes.

The first interpretation, which Schott maintained, is ruled out by the fact that these structures arise always closely at the base of the gynoecia (see Fig. 55) and that between the individual female flowers where these clavate structures stand closely below the gynoecia, there is also still some space available. That these clavate structures are rather staminodes and not rudiments of a perigon results from their similarity, already discussed earlier, with the staminodes of the sterile male flowers. Further, a conclusive factor is the previously mentioned relation in *Schismatoglottis*, in which the individual staminodes do not have such an exclusively definite position as in *Homalomena*. While in the upper region of the female inflorescence the position of each staminode in front of the gynoecium is very distinct, in the lowest part of the female inflorescence there is seemingly irregularity with respect to the arrangement of the staminodes; it seems that sometimes there are two staminodes in front of a gynoecium and in other cases they seem to be quite absent. This apparent irregularity

stems from the fact that in the lower region the slender threads of the staminodes slide through the lower-lying gynoecia so that their clavate heads lie next to one of the more basal gynoecia.

Homalomena, like *Spathiphyllum*, is represented in the Indian {=Indo-Malayan} Archipelago and in tropical America, but in contrast to the latter genus, is more weakly developed in America; here occur some interesting species with underground stems, which were described by Linden and André as *Curmeria* but by Regel and myself were referred to *Homalomena*. The male flowers here are frequently 5 – 6- androus; two species, *H. Wendlandii* and *H. peltata* possess staminodes, as in the species of the Old World, but the others, *H. picturata*, *H. Roezlii* and *H. Wallisii* do not develop them. Connected to these is then *Adelonema erythropus*, also native to South America, which perhaps belongs to the former genus {i.e. *Homalomena*} but in the only existing specimen in the Munich State Herbarium {M} the male flowers are so crushed and partly destroyed that it is difficult to determine their structure {and} it seems that the stamens are connate into synandria.

Chamaecladon is the genus closest by far to *Homalomena*; here the placentae are completely axile {central}, while in *Homalomena* the inward-projecting placentae approach the centre, the ovules are anatropous and each female flower is provided with a single staminode.

The South African genus *Zantedeschia* Spreng. (*Richardia* Kunth) is not very closely connected to these very near[-related] genera but sufficiently so; in both *Z. aethiopica* and *Z. albomaculata* the ovaries are surrounded by inverted wedge-shaped or spathe-shaped, apically thickened organs, which in the uppermost female flowers are sometimes represented by fertile stamens, {and} in which in transverse sections their alternation with the 3 – 4 carpels of the gynoecium is evident; therefore there is no doubt that here we are dealing with staminodes which are functioning as a perigon. The densely crowded male flowers are formed from 2 or 3 stamens. *Philodendron* stands nearer to the genera first discussed than *Zantedeschia*, and its species appear to be just as diverse in South America as those of *Anthurium*, but in the flowers show a greater variation than in the latter genus. Usually the lower part of the inflorescence is purely female and the upper purely male and formed of 3 – 5 androus flowers, {but} where the long-persistent spathe is constricted and below the constriction the spadix is covered with sterile flowers formed of staminodes; usually the staminodes have the form of stamens but are thinner and often somewhat longer so that the part of the

inflorescence taken up by them is somewhat more strongly swollen. Physiologically these sterile male inflorescences only have the function that they seal up most of the entrance to the cavity which encloses the female inflorescence; however they are also present in species in which the spathe completely opens. In the female flowers staminodes are found only exceptionally, as in *Ph. brevilaminatum* Schott, of which I have copied a part of the female inflorescence of Schott's illustration (*Aroideae Maximiliana* Plate 37) in Plate V Fig. 57 at a smaller scale. The peculiar development of the gynoecium in which individual carpels become almost {completely formed} shows that we are dealing here with an abnormal formation; nevertheless it is interesting that here staminodes are formed and indeed in greater numbers. The gynoecia are of the greatest diversity. The number of carpels is here still more variable than the number of stamens in the male flowers; in most cases the ovary is 4 – 6 –locular, as in *Ph. Ochrostemon* for example a frequently cultivated species, but in *Ph. Wendlandii* we find 7-locular ovaries, 8-locular in *Ph. acutatum*, 8 – 10-locular in *Ph. eximium*, 7 – 10 –locular in *Ph. modestum*, 9 – 12-locular in *Ph. disparile*, 5 – 11 –locular in *Ph. tripartitum*, 14 – locular in *Ph. Williamsii*, 9 – 11-locular in *Ph. speciosum*; as emerges from these data, the number of locules is often variable in the same species and on this account cannot be given any great weight in the separation of the Sections. On the other hand the also very variable number of the ovules in the locules is of greater constancy in the same species and also within the larger groups of related species [Formenkreise]. In most species the axile placenta is completely covered with ovules, in *Phil. Ochrostemon* and *Ph. Oxycardium* with 4 – 6 rows, and in many {species} with 2 rows, {but} in the species of Sections *Meconostigma* and *Sphinctrostigma* with only a single row. Next are the species in which the ovules are located only in the lower part of the ovary locules, thus 3 – 4 in *Ph. panduraeforme*; still other species have several ovules only at the base of the ovary, thus *Ph. Melinonii*, while in *Ph. eximium* only 3 – 4 stand at the base of each locule. Finally we find in *Ph. Linnaei* and related species only two at the base of each locule and in *Ph. tripartitum*, *Ph. Fenzlii*, *Ph. advena*, *Ph. Lindenii*, *Ph. erubescens* only a single ovule. In spite of all these differences a separation of the many species into individual genera is not allowable since there are always intermediates. However these are lacking between *Philodendron* and its next most related genus *Philonotion*, where the female flowers consist of a unilocular gynoecium with a basal ovule, that is hemi-anatropous as in *Philodendron* and is borne on a long funicle. Also in

Philonotion the male flowers are formed of only two stamens, and in the place of the well developed staminodes of *Philodendron* we find here only indistinct protuberances as in the appendices of some *Aroideae*, e.g. *Helicophyllum*.

The insufficiently known genus *Thaumatophyllum* Schott is also closely related to *Philodendron*; for we know at least this much from its single species occurring in northern Brazil, distinguished from all other *Philodendroideae* by the pedatifid leaf, that numerous orthotropous ovules are arranged in two rows in the placentae in the very probably 4-locular ovary.

The following genera are not so closely related [nicht so nahe verwandtschaftlichen Verhältniss] to those previously described as the latter are amongst themselves; however I know of no other subfamily of Araceae to which I could link them more closely, since their anatomical structure and venation bring to mind to a high degree those of the genera just described. The West African genus *Anubias* is rather similar to *Homalomena* in habit, but is characterized in its venation by the fact that extremely numerous slender transverse veins occur between the almost completely parallel primary and secondary lateral veins. The broad, axile placenta is very densely covered with anatropous ovules - the latter are somewhat similar to those of *Homalomena* - the 2-locular gynoecea have no staminodes.

Densely crowded sterile male flowers, i.e. synandrodes in which no pollen develops, follow immediately after the female flowers. Above these stand less dense, numerous synandria formed from 4 – 5 connate stamens.

The genus *Typhonodorum*, until now found only in Madagascar, reminds one very strongly of *Zantedeschia* in the constitution of its leaves, with which it also agrees in growth [habit?]; unfortunately up to now there are available only few and deficient specimens of both species of the genus in herbaria. The ovaries of the female flowers are crowned by a 4-lobed stigma in *T. Lindleyanum* and by a 3 – 6 lobed stigma in *T. madagascariense*; although the ovaries are unilocular and include at the base only 1 or 2 anatropous ovules, I believe nevertheless that I can presume that here several carpels are involved in the {formation of the} ovary because the ovules stand in the middle of the ovary and the stigma lobes protrude strongly and then also because the male flowers are synandria formed from a larger number of stamens, 4 – 8. Synandrodes are situated both between the female and fertile male flowers and above the fertile male flowers, which sometimes are also represented by a group of separated staminodes. In *Typhonodorum madagascariense* individual staminodes also

occur around the female flowers, as in *Schismatoglottis rupestris*. Finally the North American genus *Peltandra* remains {to be discussed}, which in leaf formation and growth brings to mind *Richardia*, while the inflorescence shows similar structure [ähnliche Verhältnisse] to *Staurostigma*. In *Peltandra undulata* approximately the lower sixth of the cylindric spadix is covered with female flowers, of which the unilocular gynoecium bears a sessile, hemi-anatropous ovule situated on a parietal placenta and which is surrounded by a 4 – 5 – edged integument which leaves only the style and stigma free; after these female flowers follow immediately synandria formed of 4 – 5 stamens which cover the spadix in regular parastichies up to a little below the apex; the uppermost synandria are however not differentiated, but in their place a not very distinct appendix is developed by the merging of their primordia. The morphological significance of the integument surrounding the ovaries becomes immediately clear if one investigates the inflorescence of *Peltandra virginica*. Here. After the female flowers follow syandria which are similar to those standing higher up, bearing 2 – 3 anthers but in the middle they are provided with a conical protuberance which corresponds exactly to the style of the female flowers; there is no doubt that here, stamens and staminodes have fused with the rudimentary ovary into a structure which represents a rudimentary bisexual flower. It thus follows that the integuments of the ovaries are synandrodes formed of several staminodes.

In my first treatments on the Araceae I distinguished a subfamily *Aglaonemoideae*. I could not distinguish this {taxon} anatomically from the *Philodendroideae* nor did the venation show any good difference, only the seeds very clearly distinguished themselves from those of the *Philodendroideae* by the lack of endosperm and the thick macropodal embryo, as we find in many *Monsteroideae*. In the latter subfamily however, there are genera with albuminous seeds often stand very close to certain genera lacking endosperm in the seeds, and so it is not possible to form two subfamilies according to the constitution of the seeds {alone}; on this account, the otherwise so significant character of the the endosperm content of the seed be set aside. So, the genera *Aglaonema*, *Dieffenbachia* and *Aglaodorum* are not closely related to the true *Philodendroideae*; but their phylogenetic connections [verwandtschaftlichen Beziehungen] to them are no less than those of *Typhonodorum*, *Peltandra* and *Anubias*, about which we still know nothing of their embryo structure.

Dieffenbachia was placed by Schott in a tribe with *Staurostigma*, *Mangonia* and *Taccarum*; but these plants have so little in common that this placement is

incomprehensible given the otherwise well-recognized expertise of Schott. Growth form [Wuchs], shape and venation of the leaves and also the anatomical constitution are like those of many *Philodendron*; at first sight it seems remarkable that the inflorescence on its dorsal side is largely adnate to the spathe and only the male inflorescence is free, as in *Staurostigma*. However, it also occurs in some *Philodendron*, e.g. *Ph. speciosum* and *Ph. bipinnatifidum* that the lower part of the female inflorescence is adnate to the spathe. The gynoecia of *Dieffenbachia* are formed from 2 or 3 carpels, and in each locule we find one anatropous ovule at the base, the micropyle of which is not always turned in the same direction. The structures surrounding the gynoecium are staminodes, as a glance at our Fig. 59, Plate V shows. In bicarpellary gynoecia there are usually 4 [staminodes] present, but in tricarpellary ones {there are} 3 – 6. Between the female and male inflorescences then follow a few sterile flowers, formed out of a few staminodes, the latter sometimes surrounding an empty space and sometimes more densely crowded together; the fertile male inflorescence is hardly different from that of most *Philodendron*. Just as *Dieffenbachia* is close to *Philodendron*, so is *Aglaonema* to the genera *Homalomena* and *Chamaecladon*. The unusually few female flowers are completely naked, the gynoecium appears peculiar because of its funnel-shaped stigma and encloses with its thick walls a single basal, almost sessile anatropous ovule, that as in *Dieffenbachia* develops into a seed lacking endosperm. The male flowers consist usually of only stamens standing opposed to each other with lateral thecae. Here should also be placed *Aglaodorum Griffithii*, but which is still insufficiently known. The relatively large ovaries and probably formed out of 4 carpels, since the stigma is 4-lobed and in the case of ovaries with 2 locules, there are 2 lobes above each locule; it is frequently the case however that only a single locule develops; in each case we find in the locule only one single anatropous ovule. Next to individual gynoecia there are prismatic staminodes. The male flowers are still insufficiently known.

If I now combine the *Aglaonemeae* with the true *Philodendreae*, the summary on p. 317 gives a idea of the principal development in this taxon.

13. Colocasioideae

Colocasia and the genera related to it form a very natural subfamily [Gruppe] which stand near to the *Aroideae* and *Philodendroideae*, but are distinguished from both by the peculiarity that the secondary lateral veins between the primary lateral

veins are always connected by a clearly prominent collective vein. In addition to this, in most anastomosing laticifers [anastomosirende Milchsaftgefäße] are present and that in all the stamens form synandria. Since the anastomosing laticifers do not occur in all *Colocasioideae* and synandria also occur in other *Araceae*, the venation remains as the only completely {characterizing} character.

Neither perigyniate flowered, nor bisexual flowered genera are known in this subfamily; however there is a genus with staminodes in the female flowers, *Steudnera*¹³. In *St. colocasiaefolia* the spadix is only short in relation to the spathe, completely covered with flowers, up to 2/3 with female flowers and up to 1/3 with male ones. The latter are formed from 3 – 4 stamens which are connate into a synandrium, and the gynoecium of the female flowers is formed from 2 – 4 carpels with parietal placentas, on which several hemianatropous ovules are situated. Around the gynoecia of the lower flowers we find staminodes, sometimes regularly alternating with the carpels of the gynoecium, sometimes in fewer number than the carpels. Most other *Colocasioideae* have a spadix which is not continuously covered with fertile flowers, but bears synandrodies on a more or less long stretch between the fertile female and male flowers; {the synandrodies} often assume a rather peculiar shape as a consequence of both the significant elongation of the spadix at this place as well as the pressure exerted by the spathe which is tightly constricted there, but they always, by comparison with the lowermost synandria, turn out to be synandrodies, with little doubt. As in *Steudnera*, so also in *Gonatanthus* the spadix is covered with flowers up to its blunt apex, similarly in *Remusatia* which also agrees with *Steudnera* in the placentation. There are no staminodes next to the gynoecia in the last-mentioned genera, but on the other hand there definitely are pistillodes present, since the lowermost female flowers turn into structures lacking ovules; that these structures are not staminodes is clear from their position, as shown for example in Plate V, Fig. 60, where a part of the female inflorescence of *Gonatanthus sarmentosus* is shown flattened out. These three genera are otherwise closely related [in naher verwantschaftlicher Beziehung] are similar especially in the peltate leaves. *Alocasia* and *Colocasia* are linked to them, but are characterized by the development of the so-called appendix. In *Alocasia*, especially *A. macrorrhiza* and *A. odora*, and also in *A. indica*, one can convince oneself without difficulty that this appendix consists of

¹³ Exceptionally I found also individual staminodes belonging to the somewhat more basal gynoecia in *Xanthosoma helleborifolium*; this state is illustrated in Plate V, Fig. 62.

rudimentary stamens. In all these species, after the uppermost fully developed stamens there follow those which bear pollen-bearing thecae on the lower side {facing the spadix base} while on the side facing the spadix apex they are lacking; after these follow the synandroides which usually repeat the shape of the synandria; but they are connate with their lower parts and also here and there have distortions and furrows on their flattened apex {of the synandrode} which delimit the individual staminode halves {i.e. partially free parts of the staminodes that form the synandrode}. Higher up the synandria are still more distorted in the longitudinal direction of the spadix and still more fused together with one another, so that the furrows which delimit the individual synandria from one another are no stronger than those between the staminodial lobes; in this way arises along the whole spadix appendix a labyrinth of fine snake-shaped, tortuous mostly interconnected furrows in which one can no longer detect the borders of the individual synandroides. *Alocasia*, as in *Gonatanthus*, has a 3 – 4 –gynous but unilocular ovary with basal placentas, while *Colocasia* possesses 2 – 4 parietal placentas. In *Col. Antiquorum* pistillodes occur, as in *Gonatanthus*, which however are not, as in the latter genus, situated only at the base of the female inflorescence, but everywhere throughout it, occurring between the normally developed pistils (Plate V, Fig. 61). These structures show themselves to be pistillodes, not only by their position, but also through the fact that they are not rarely papillate on the apex like the stigmas of fertile pistils. The uppermost part of the female inflorescence is taken up exclusively with pistillodes, and synandrodia follow immediately after these up to the upper limit of the constriction. We see the uppermost synandria, as in *Alocasia*, {progressively} turning into synandroides; but the synandroides are only recognizable in the lowermost part of the appendix, {because} they are so completely fused over most of the appendix that not even the furrows separating them are visible; here the differentiation is further retarded than in *Alocasia*; nevertheless, the whole appendix is, just as clearly as in *Alocasia*, an axis clothed with the primordia of staminal structures. The length of this appendix is very variable in the different forms of *Colocasia Antiquorum*, even to being reduced to a small apical stub, as in var. *acris* which occurs in cultivation in Australia. The appendix in *C. gigantea* (*Leucocasia gig.* Schott) is also very small, but here shows numerous furrows like the appendices of *Alocasia*.

In the Old World, apart from these {afore-mentioned} genera, there occurs also a peculiar genus, *Schizocasia*. The magnificent *Sch. Portei*, on which Schott based his

genus, is native to the Philippines and cultivated in some botanical gardens, but has never yet come into flower. Beccari then discovered in New Guinea a plant named by me as *Sch. Acuta*, the flowers and fruits of which show it to be a member of the one of the previously mentioned genera. Since, however, the flowers and fruits of *Schiz. Portei* are still not known, so for the moment doubt remains whether the characteristics of “*Sch. acuta*” apply at all to the genus *Schizocasia*. The gynoecium is unilocular, as in *Alocasia*, but the basal ovules are not hemi-anatropous or orthotropous but completely anatropous. The entire upper part of the spadix is taken up by distinctly separated synandrodes which are strongly elongated in the long axis of the spadix. The ovule of the little known genus *Hapaline* is also anatropous, which however, could only be placed in another higher taxon [Gruppe] with difficulty; one could possibly consider the *Areae*; but all the genera of this taxon possess orthotropous ovules and never have such synandria as occur in this subfamily of *Colocasioideae* and in *Hapaline*. On the lower part of the spadix, which is dorsally “connate” to the spathe, we find some rather laxly arranged, unilocular gynoecia one parietal ovule; apart from the apex, which is covered with about 3 synandrodes, the male inflorescence is covered with elongated rhombic synandria; only few synandria occur at the lower boundary of the male inflorescence.

The genera *Caladium* and *Xanthosoma*, which are native to the New World, offer less that is remarkable in their flowers. The inflorescences, as in *Remusatia* and *Gonatanthus*, are covered with fertile synandria to the apex, and we find only synandrodes in the portion surrounded by the spathe constriction; in the ovary, the carpel margins project so far inwards that they give rise to either completely axile or subaxile placentas, which bear several anatropous ovules; also the development of the seeds is similar to that of the *Colocasioideae* of the Old World. *Xanthosoma* (incl. *Acontias*) is only different from *Caladium* in that the style below the stigma is expanded into a disc-like structure and the disc-like structures of neighbouring flowers are connate with each other. *Chlorospatha*, of which I have described a species *Chlorosp. Kolbii* from Colombia, is also closely related to *Xanthosoma*; this genus is distinguished from *Xanthosoma* by the fact that the spathe is not distinctly separated into tube and blade, the gynoecia are quite free and not connate in virtue of the ring-like expansion of the style, that the ovules are situated in the lower part of the locules, and that the upper gynoecia and the synandria are grouped into whorls which are somewhat distant from one another.

After much reflection I must now place the genus *Syngonium*, which earlier and not without expressing reservations, I had joined to the *Lasioideae*, in the *Colocasioideae*. The connection with the *Lasioideae* previously seemed to me based on lack of endosperm in the seed; I thought I should give more importance to these embryological conditions than to the anatomical structure which agrees with that of the *Colocasioideae*; for the species of *Syngonium* possess anastomosing laticifers [Milchsaftgefäße] as distinctly as *Xanthosoma*; and the leaf venation also agrees better with that of the *Colocasioideae* than with any other subfamily; the inflorescence also agrees with those of *Caladium* and *Xanthosoma*. The synandria diverge from those of the other *Colocasioideae* only in that the individual stamens stand out more independently. On the other hand the gynoecia are very remarkable, formed from 2 – 3 very thick carpels, 2 – 3 locular, sometimes unilocular by abortion, including a single short anatropous ovule in each locule that develops into a seed lacking endosperm, and furthermore the gynoecia are all connate with one another. The genus *Porphyrospatha*, which I have separated off from *Syngonium*, is essentially different in that the gynoecia are free and in each locule there are 1 – 2 ovules in the middle of the axile placenta. Whether the seeds have the same nature as in *Syngonium* is still to be determined.

Ariopsis, a remarkable genus, remains {to describe}, which I previously classified as a member of the Aroideae in its own subtribe. It is in fact a very remarkable genus which is not closely related to any other. The cordate leaves of *Ariopsis peltata* which are cultivated repeatedly in our glasshouses, have a venation which is not so typical as in the true *Colocasioideae*, and the collective veins are not so much in evidence; branched laticifers also do not occur in *Ariopsis*. Finally the floral structure is different from that of the *Colocasioideae*. The whole inflorescence is very small, barely 1.5 – 2 cm long, the spathe has no constriction as in true *Colocasioideae*, but instead opens over its whole length. The female inflorescence is reduced to a few gynoecia (see Plate V, Fig. 63, 64). Each gynoecia is usually formed of four carpels, the placentae are completely parietal and covered with several orthotropous ovules in two rows (Fig. 66). However the male inflorescence is very remarkable. Here we have the only case in our family where the spirally arranged male flowers are connate with one another, something comparable {to the situation} in *Cryptocoryne* and *Syngonium* in which the female flowers are associated together [mit einander consociiren]. However the connation is here even more complete. Figs.

63 – 65 illustrate the highly peculiar behaviour of this plant. The circular openings immediately stand out, which are surrounded by a slightly prominent parapet. The longitudinal and transverse sections through the spadix, particularly the latter, allow the remarkable structure to be seen; the circular openings lead to deep cavities (Figs. 65 and 66h), into the narrowest part of the cavity open usually 6, sometimes 8 small holes (Fig. 65o); these holes are those through which the pollen emerges from the ellipsoid anthers. In Schott's *Genera Aroidearum* (Tab. 35), these openings of the anthers are drawn in such a way that one could think that two anthers together dehisce at this point. This is not correct, {in fact} each hole corresponds to only one anther even in the young stages. Also, I consider inaccurate the manner in which Schott here interprets the individual flowers. In his opinion, the tissue masses which in transverse section are rather rhombic, and which lie between each four holes, always belong to one flower, and thus the anthers of four different flowers must open into each cavity. Now we find however usually six and sometimes eight openings. Transverse sections through the circular parapets around the holes yield structures as in Fig. 67.

Furthermore, if Schott's view was correct, the number of holes in the lowermost cavities would be smaller; for there only two flowers would meet. But we find in the lowermost cavities of the spadix just as many, usually six, {holes corresponding to} anther openings {stomia}. On this basis, only one other interpretation remains, namely that here, somewhat as we have seen in *Taccarum Warmingianum* (Fig. 14), the stamens of one flower, standing in a circle, are connate [mit einander consociirt sind]. Since in this case however, not only are the stamens "connate" laterally with one another but also dorsally with those of the neighbouring flowers, so the dorsal anthers are lost as a result of this connation, and only those on the anterior side are fully formed, i.e. the anthers opening into the cavities. This development of the stamens must have become the rule so that two dorsal anthers of the free stamen of the lower flowers were also lost.

The phylogenetic relationships [verwandtschaftlichen Beziehungen] of the Colocasioideae are expressed in the following summary. {see tables}

14. Monsteroideae

While the majority of the Araceae have laticifers [Milchsaftgefässen] of different kinds, a minority of the genera are characterized anatomically by their absence; among these are some which have in their tissue, more or less abundantly,

the well known, two-armed or H-shaped trichosclereids [Spicularzellen], which grow out of the tissue layers that border the intercellular spaces and into the intercellular passages and because of this are often termed intercellular hairs. I have grouped together the genera characterized by this latter characteristic into a subfamily *Monsteroideae*; for although these trichosclereids increase the strength of the organs in which they occur, I cannot regard them as an exclusively mechanical element, since they are lacking in many genera which have the same growth conditions. In the following I will also show that in fact the genera grouped in this subfamily show by their floral structure that they belong to a natural group of related taxa [natürlichen Verwandtschaftskreise]. With the exception of the genus *Spathiphyllum*, some *Rhodospatha*, *Stenospermation*, and *Holochlamys*, the genus proposed by me in “Malesia”, the *Monsteroideae* are climbing plants like most *Philodendron* and some *Anthuria*; apart from the trichosclereids, which occur in all of them in the stems, petioles and frequently in the pistils, they also all agree in that they surpass the other *Araceae* in tannin content and on this account with the exception of the thin-leaved *Spathiphyllum* and *Rhodospatha* become quite black-brown on drying. The two genera *Spathiphyllum* and *Holochlamys* essentially agree in their floral diagrams [stimmen diagrammatisch ... überein] with many *Lilaceae* as do also *Anthurium*, *Pothos*, *Acorus*, *Dracontium*. When the older authors grouped these genera as the *Orontieae* this is just as unnatural as when they were raised up as a tribe of the *Lilaceae*; indeed the *Liliaceous Rohdea japonica* has often been confused with *Orontium aquaticum*. Within the genus *Spathiphyllum* itself we have quite a degree of diversity. In most species the perigon is made up of free tepals [das Perigon ist getrenntblättrig], but in some (*Sp. cannaeforme*, *Sp. commutatum*, *Sect. Massonia*) the tepals are connate [verwachsenblättrig], usually formed from 6 tepals, sometimes from 8. Two isomerous stamens whorls and one such carpel whorl correspond to the the two perigon whorls. The locules of the ovary contain in some species 6 – 8 axile, anatropous ovules, in some two, and in some (*Sect. Amomophyllum*) only 1 – 2. The seed contains endosperm in all species. *Holochlamys* is distinguished from the species with a connate perigon only by the fact that the perigon is formed from four connate [consociierten] tepals and that numerous anatropous ovules are all attached to the base of the unilocular ovary by long funicles. The circumstance that the ovules are all turned away from the centre and towards the wall of the ovary, as well as the 4-lobed stigma imply that the gynoecium is not monocarpellate but very probably formed

from two or four carpels. The genus *Spathiphyllum* is one of the few genera of Araceae which occurs in the tropics of both the Old and New Worlds in closely related forms. *Spathiphyllum commutatum* from the Philippines and the Celebes, and at the same time the only species of the genus in the Old World, is very near *Sp. cannaefolium* from Brazil; the genus *Holochlamys*, however, has been discovered in New Guinea by Beccari. Whether the seed in this genus agrees with that of *Spathiphyllum* is not yet known. No other known genus of the Monsteroideae possesses a perigon. If we ignore this however, then we shall soon see that in *Rhodospatha* we have a genus that has so much in common with *Spathiphyllum* as regards its habit, that non-flowering specimens of the species with short internodes are easily taken for *Spathiphyllums*. The flowers are composed of 4 stamens and a gynoeceum composed of 2 carpels, with numerous anatropous ovules on the axile placentae which develop into amphitropous, somewhat flattened seeds containing endosperm. The genus *Anepsias*, separated by Schott but perhaps better included in *Rhodospatha*, is distinguished by the fact that in the same spadix there are both dimerous and 3 – 6 – merous pistils. While in the dimerous pistils the ovules are situated on the septa in several rows, we find in the pleiomerous pistils only two rows of ovules in each locule, and thus the number of ovules is not very much increased by the increase in carpel number. The genus *Stenospermation* is just as closely linked to *Rhodospatha*, and differs in its floral structure essentially only in the fact that the similarly anatropous ovules arise only at the base of the septum but in larger numbers, more than 4 [{}] meist zu 4]. All these genera show many similarities in their leaf structure: the always more or less lanceolate leaves are never divided, the primary lateral veins are numerous and almost parallel, the secondary lateral veins diverge in their direction only a little from the the prinar veins; also in all of them there is a long leaf sheath present.

The leaves of the younger generation in *Monstera* also show the same condition, but with the difference that the primary lateral veins are more widely distant from one another, and as a consequence the secondary and tertiary lateral veins have a rather more oblique course; the leaves of the older generations show the well-known formation of perforations and pinnate division [Fiederung], as a result of the retardation of growth and tearing in certain places, which however, has nothing to do with true pinnate division that we find in some *Philodendron*. In its leaf development, therefore, *Monstera* is strongly connected to the previously mentioned genera. The

spadices, as in all genera of this subfamily are covered from the base to apex with flowers; however in *Monstera* we see, as in *Urospatha* (see p. 176) the lower flowers become sterile {with} the stamens rudimentary and the differentiation of the ovules in the ovaries suppressed. The fertile flowers are different from those of the genus *Stenospermatum* only in that at the base of the locule the ovules are developed in pairs rather than in fours. The structure of the ovules themselves, of the stigma and the anthers shows great similarity in all these genera; only the seeds are essentially different in that they do not enclose a cylindric embryo surrounded by endosperm, but a stout, ovoid embryo which has absorbed all the endosperm. We find in other natural related groups [natürlichen Verwandtschaftskreisen] as in the *Philodendroideae* and *Aroideae*, a great similarity in the nature of the seeds; here we see in closely related forms a prominent difference (the nature of the embryo in *Stenospermatum* and *Holochlamys* is still unknown); but we will meet yet some closely related genera in this subfamily which diverge from one another in this way. The species of *Rhaphidophora* of the Old World are in their young state hardly different from the *Monstera* species of the New World, the inflorescences and the individual flowers also show great similarity and the fruits also behave like those of *Monstera* in as far as the broad, basally rhombic and upwards conically narrowed apex of the pistil is shed. The ovules are borne on a long funicle, like those of *Holochlamys*, and form two rows, or rarely more, on parietal placentae which project far into the ovary or frequently meet in the centre; in essentials the structural relations [Verhältnisse] are thus similar to those of *Rhodospatha*. The species of *Epipremnum* are confusingly similar to *Rhaphidophoras* and not identifiable generically without analysis of the flowers. Instead of a bi-locular ovary we find here a unilocular ovary with a parietal placenta; this latter is located on the side towards the apex of the spadix, as in most *Araceae* with unilocular ovaries. The species, which Schott knew possessed only two ovules at the base of the placenta, on the other hand species collected later by Beccari became known to me in which two rows of ovules are situated on the placenta as in *Rhaphidophora*; however the seeds are completely different, not numerous small and thin-walled, but in smaller numbers, large with a thicker testa and more endosperm; the seed and embryo is also distinguished sometimes by a tendency to amphitropy. *Scindapsus* shows a very similar structure of the seeds, a genus which diverges from *Epipremnum* only in that only a single basally-located anatropous ovule is present in

the unilocular ovary. *Cuscuaria* has just such a structure of the ovary, but we do not yet know the nature of the seed in this genus.

From this information it follows that the interrelation of all the genera belonging to the *Monsteroideae* is very profound; the following summary allows the connections of the genera to one another to be quickly seen. {see table}

15. Pothoideae

In the subfamilies [Gruppen] already dealt with, it was not difficult to ascertain an inner coherence between the genera; within the subfamily of the Pothoideae {however} which show no outstanding histological peculiarity, this {coherence} is more difficult to demonstrate. While on the one hand most of the genera of this subfamily, due to the presence of a perigon and the isomery of the flowers, approach the Type which in the other subfamilies we were justified in regarding as the starting point of {their} development [als Ausgangspunkt der Entwicklung], on the other hand no genus is known in which numerous parietal or axile ovules are present in the gynoecium; rather the ovules mostly limited in their number and position. As regards their vegetative parts, a great diversity is manifest in this subfamily, as in the *Monsteroideae*.

Acorus diverges the most from the other genera, by its underground rhizome, its sword-shaped leaves, which recur only in the genus *Gymnostachys*, its peculiar ovules, whose outer integument is cut into a fringe at the micropylar end. The genus *Gymnostachys*, which usually brings to mind *Acorus* because of the narrow grass-like leaves, in fact is not closely related to the latter. It has “roots” with spindle-shaped, swollen tubers; one can find nowhere any satisfactory information about the duration of the growth period. In the place of the underground branching of *Acorus* here there is a much-branched aerial {stem}, but with shortened internodes (see my paper: *Vergl. Untersuchungen* p. 171, Taf. I, Fig. 3).

The spirally arranged flowers are somewhat more loosely arranged on the pendent spadices; their gynoecium is oligomerous, unilocular, and contains only a single ovule, that as in *Acorus* hangs from the apex of the locule and as in that genus develops into a seed containing endosperm.

The genus *Anthurium* has a very uncomplicated condition, 5 dimerous whorls {in the flower} and in each locule of the ovary two anatropous ovules inserted in the

middle of the septum, of which frequently one aborts and in most cases (except in sect. *Tetraspermium*) one matures into a seed. Thus, here is the impetus towards a reduction which will be expressed in that only one ovule is produced. *Pothos*, with which *Anthurium* was in earlier times combined, possesses five trimerous whorls in each flower, in the ovaries of which a single anatropous ovule is situated as the base. The climbing, frequently branched shrubs of this genus produce very varied leaves. In the young pre-flowering stage the branches nearer the ground have shortly petiolate leaves with ovate blades, while at the flowering stage and in branches higher up the leaves have longer petioles and lanceolate or linear blades. A plant which occurs in the area of highest diversity of *Pothos*, which was named by Schott as *Amydrium humile*, possesses only short little stems, as in some *Anthuriums*, and at the apices of these long-petiolate, cordate leaves which in their shape are similar to the leaves of some non-flowering *Pothos*, but on the other hand show agreement with the leaves of some *Anthuriums*. The spathe and spadix are similar to those of many *Pothos*, but here the spathe is not reflexed as in *Pothos* and most *Anthurium*, but remains, it seems, upright and enclosing the spadix for a long time. Perhaps this is correlated with the fact that the flowers are naked. For the rest they agree very much, apart from the dimery, with those of *Pothos*. Still more closely related to *Pothos* is the genus *Pothoidium*, which is distinguished only by the oligomerous, unilocular gynoeceium, which contains a solitary basal ovule in the single locule. A direct descent from *Pothos* is in this case hardly to be doubted. *Anadendron* also belongs to this group [Verwandtschaftskreis], although Schott has placed this genus in the *Monsterinae*. The perigon is here a single connate structure [verwachsenblättrig]; the gynoeceium, which is somewhat compressed from above and obconic, contains only one anatropous ovule in its single locule, which is not however positioned to the side, as in *Pothoidium*, but rises up from the floor of the locule. The genus *Heteropsis* stands further away from *Pothos* than the genera so far mentioned, even though the manner of growth [Wachstumsverhältnisse] are rather similar. Although the spathe [Scheide] is soon shed, the flowers are nevertheless naked. Diagrammatically, they correspond to those of *Anthurium* with the difference that the perigon is lacking; the ovules are however more similar to those of *Pothos* and like those of the latter are situated at the base of the septum, but instead of being single they are in pairs. The African genus *Culcasia* strongly agrees with *Heteropsis* in anatomical structure; its branching pattern follows that of *Anadendron*, and similarly its leaves are similar to those of the

latter genus. On the other hand the floral structure is substantially different from that in all the other genera of the subfamily discussed here. The flowers are unisexual; the lowest are somewhat loosely-packed female flowers composed of 2- or unilocular gynoecea each with one basal anatropous ovule in the locule and with a thicker, discoid, indistinctly 4-lobed stigma. Nothing can be seen here of aborted stamens, nor is there any trace in the male flowers of a gynoeceum; we can therefore presume that reduction {has occurred} at the most on the basis that in other Araceae unisexuality of the flowers is recognized as a consequence of reduction. The stamens of the male inflorescence are particularly densely crowded, but one can see at first glance that every group of four belongs to a flower. As in most naked male flowers of the Araceae, the stamens are also here very thick and fleshy with the thecae {occupying} almost the entire length of the stamens.

Just as so little close connection to any other genus can be ascertained in *Culcasia*, is this possible for *Zamioculcas* and *Gonatopus*, which are only closely related to one another. Both monotypic genera possess a tuberous stock, but they are not closely allied to the other Araceae which grow in the same way; the constitution of their leaves is substantially different from all other Araceae; in *Zamioculcas* they are once-pinnate, and in *Gonatopus* bipinnate and in both the individual leaflets are deciduous, and also in both the petiole abscises rather far above the base at the swollen "geniculum". I have studied the anatomy of living material of both genera, and I found none of the peculiarities that occur in the other subfamilies, no trace of laticifers [Milchsaftschläuchen]. The shortly pedunculate inflorescence is in both covered with dimerous flowers up to the apex, and their perigon is in the same condition as in *Anthurium*, also the stamens are similar to those of Anthuriums. While in *Zamioculcas* the spadix is slightly constricted at the border between the male and female inflorescences, this is not the case in *Gonatopus*. In both genera we find evidence for reduction in rudimentary perigonal organs [Sexualblättern] alongside the fertile ones. In *Zamioculcas* the bilocular ovary is either alone or sometimes surrounded by 4 or fewer stunted stamens, and in *Gonatopus* there are at most 1 – 2 staminodes without any trace of an anther and often they are completely absent; in both genera there is in each locule one short anatropous ovule, as in *Pothos* at the base of the locule on the septum. In the male flowers of *Zamioculcas* sometimes the stunted ovary contains still ovule primordia; they seem to have grown to some extent, although the differentiation of the funicle is suppressed; in the male flower of

Gonatopus the ovary is completely rudimentary, without a trace of ovule primordia. Also we find in *Zamioculcas* at the border of the two fertile inflorescences a narrow zone covered by the constriction of the spathe, which bears only flowers with somewhat smaller tepals [Perigonblättern] and completely stunted ovaries. A physiological importance has to be excluded for these flowers, they are merely reduced, and are structures that have no further use.

We have here thus the process of reduction before us to some extent; what emerges from this, as in so many other cases mentioned already, is that the classification of the Araceae according to the sexuality of the flowers is not admissible. {see table}

16. Calloideae.

To the Pothoideae I have previously {Engler 1879} assigned the four genera *Orontium*, *Symplocarpus*, *Lysichiton*, *Calla* to the Pothoideae; however, their anatomy, in which at least in living material of *Calla* and *Symplocarpus* I was able to determine the presence of laticifers [Milchsafttröhren] in the vascular bundles, excludes them from this subfamily, even though they may stand near to them diagrammatically. *Calla* and *Symplocarpus* have a spathe which separates from the peduncle [Inflorescenzaxe] a little below the spadix as in most other Araceae, while in *Orontium* and *Lysichiton* the separation takes place earlier at the base of the peduncle and the spathe [Scheidenblatt] differs only a little in its whole formation from the foliage leaves. Diagrammatically the flowers of *Lysichiton* are similar to those of *Anthurium*; in the same way [bei derselben Art] there are bi-ovulate and uniovulate ovary locules. The deep embedding of the ovary in the spadix axis is very peculiar, which however, due to the rarity of the material will not be investigated developmentally for some time; Still deeper is the ovary embedded in *Symplocarpus*; here there is only a single locule from the upper end of which the ovule hangs down. Also in *Orontium*, where a basal anatropous ovule is found in the unilocular ovary, the ovary is somewhat embedded but much less so than in the first-mentioned genera. Though in *Calla* the spathe is much more open than in *Symplocarpus*, and thus the flowers are much less protected by the spathe, no perigon is found in *Calla*, nor is any rudiment of one discernible; in other respects the thin linear stamens with relatively short anthers are similar to those of the first three genera. The ovary is here

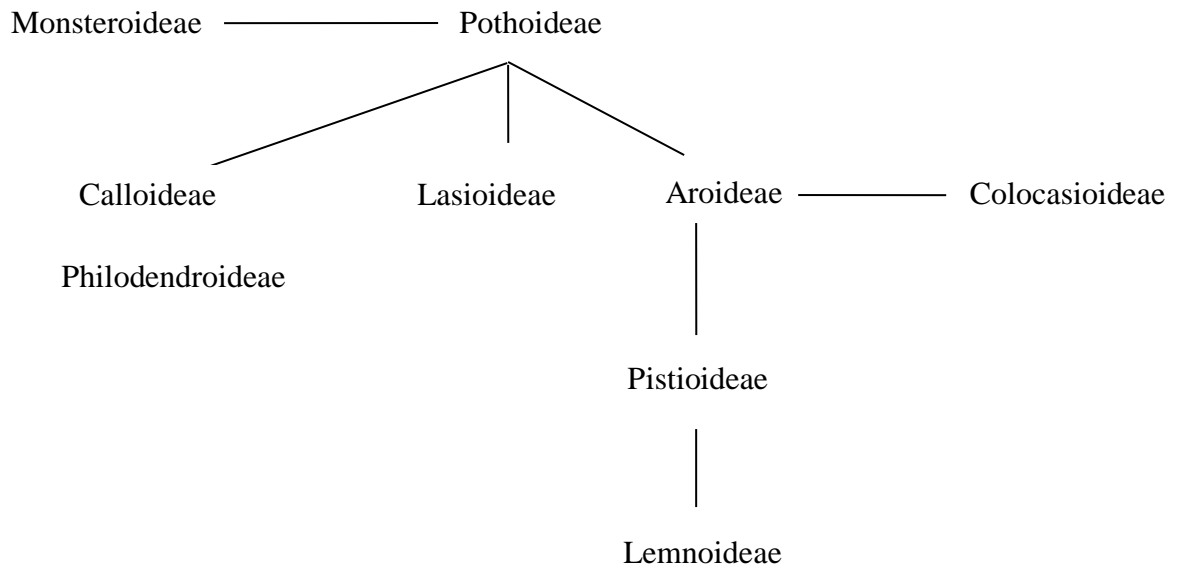
unilocular; but it is formed from 2 – 3 carpels, which as in the carpels of the Caryophyllineae are connate, and develop basal placentae on the floor of the ovary, on which 6 or 9 anatropous ovules in the manner which is usually found in such cases in the Araceae (rhaphe against the centre of the ovary, micropyle facing the lower end of the ovary wall. For the rest, we find also in *Calla* the signs of a reduction, in that the upper flowers are only male.

17. The relationships of the Araceae subfamilies [Araceen-Gruppen] to one another

Whether one recognizes the above discussed groups of Araceae as subfamilies or as tribes, is rather unimportant, as in any case they are linked together by genealogical relationships [verwandtschaftlicher Beziehung]; only in the case of the Lemnoideae can any doubt be warranted. According to the principles expressed in the first sections the subfamilies [Gruppen] must stand together in the following relationship (see below).

This arrangement gives absolutely no evidence for the age of the genera within the individual subfamilies [Gruppen], it suggests only the relative age of the subfamilies, the genera of the Philodendroideae, Aroideae, Pistioideae which now exist, could even be older than the extant genera of the Pothoideae, because they are phylogenetically already the furthest advanced. The summaries {Tables} at the end of the sections on each subfamily give sufficient information on the relationship of the genera amongst themselves.

Kiel, 15 December 1883.



18. Explanation of the Plates

All figures for which no artist is given are by the author.

Plate 1.

Fig. 1. *Hydrosme Rivieri* (Durieu) Engler. Section of the inflorescence from the border region between the male and female inflorescences. It can be seen how the parastichies formed by the female flowers continue into the male inflorescence. *c*: a flower with two stamens and a gynoecium; *a*, *b*: here can still be seen the spaces which correspond to the gynoecium; in the upper flowers *d* and *e* the stamens are much more densely crowded.

Fig. 2. *Hydrosme Rivieri* (Durieu) Engler. The same section of the inflorescence after removal of the gynoecia and stamens, clearly showing that between the floral bases there are spaces which belong to the inflorescence axis. These are marked as *a*, *b*, *c*, *e*, as in Fig. 1.

Fig. 3. *Hydrosme Rivieri* (Durieu) Engler. Section of the uppermost part of the male inflorescence with the lowest part of the appendix. The individual flowers and floral rudiments are numbered, although the numbers have no relation to the genetic sequence {i.e. order in which they developed}. See text for details.

Fig. 4. *Synantherias silvatica* Schott. Section of the male inflorescence, which shows distinctly delimited flowers. After Schott.

Fig. 5. *Staurostigma Luschnathianum* C. Koch. Section of the inflorescence from the border region, shown flattened out [aufgerollt]. The two lower rows are female flowers in which the gynoecium is enclosed by an envelope formed of staminodes and which has taken on the function of a perigon. In the third row of the lower flowers {are} flowers which show the transition from bisexual flowers into female and male ones (see text). The upper row has only male flowers.

Fig. 6. *Staurostigma Luschnathianum* C. Koch. Upper part of the inflorescence showing the transition from male flowers into the short appendix formed from fused floral rudiments. *a*: surface view, *b* LS.

- Fig. 7. *Staurostigma Luschnathianum* C. Koch. Longitudinal section of a female flower, magnified. *st.* Staminodial envelope.
- Fig. 8. *Staurostigma Luschnathianum* C. Koch. Transverse section through the ovary of a female flower.
- Fig. 9. *Synandropadix vermitoxicus* (Griseb.) Engl. Bisexual flower. Magnified.
- Fig. 10. *Synandropadix vermitoxicus* (Griseb.) Engl. Female flower with staminodes.
- Fig. 11. *Synandropadix vermitoxicus* (Griseb.) Engl. Male flower in which the stamens are fused with a rudimentary gynoecium by which they are exceeded.
- Fig. 12. *Synandropadix vermitoxicus* (Griseb.) Engl. Male flower, synandrium, in which the gynoecium has disappeared without trace; *b*: view from the apex.
Fig. 9 – 12 drawn by G. Dittman.
- Fig. 13. *Taccarum Warmingii* Engl. Bisexual flowers with 6 stamens (of which 4 have been removed) and a gynoecium formed from 6 carpels, slightly magnified.
a: side view, *b*: TS.
- Fig. 14. *Taccarum Warmingii* Engl. Male flower, in which the stamens are still separate.
- Fig. 15. *Taccarum Warmingii* Engl. Male flower in which the stamens are connate into a synandrium.

Plate II.

- Fig. 16. *Spathantheum Orbignyianum* Brongn. Inflorescence, magnified three times, dorsally adnate to the spathe. From *a – b* only female flowers, each with staminodes, from *b – c* two outer rows of female flowers and two inner rows of synandria, from *c – d* synandria only. Drawn by G. Dittman after Schott.
- Fig. 17. *Spathicarpa sagittifolia* Schott. Inflorescence in which two-membered whorls alternate with three-membered ones above and in the middle, while below only two-membered whorls are found. On the right the position of the individual flowers is shown more clearly after removal of the anther heads. Drawn by G. Dittman.
- Fig. 18. *Spathicarpa sagittifolia* Schott. Another inflorescence of the same plant, in which almost throughout, from top to bottom, two-membered whorls alternate with three-membered ones; only right at the top some two-

membered whorls alternate with one another; on the right the same inflorescence after removal of the anther heads.

Fig. 19. *Spathicarpa sagittifolia* Schott. Lower part of the inflorescence shown in Fig.

17, at greater magnification, showing the unequal mery of the synandria and the abortion of some staminodes on the two outer sides.

Fig. 19a. *Spathicarpa sagittifolia* Schott. Synandrium, enlarged. *b, b*: the two thecae of a stamen.

Fig. 20. *Spathicarpa sagittifolia* Schott. Longitudinal section through a young gynoecium, showing the still weak development of the lobe arising from the stylar canal.

Fig. 21. *Spathicarpa sagittifolia* Schott. Longitudinal section through an older gynoecium. *a*: the section is made in the same direction as in Fig. 20. *b*: section made in a plane perpendicular to that of *a*.

Fig. 22. *Spathicarpa sagittifolia* Schott. Ovule from the stage shown in Fig. 20, at high magnification. Figs. 20 – 21 drawn by G. Dittman.

Fig. 23. *Gorgonidium mirabile* Schott. Female flower, magnified.

Fig. 24. *Gorgonidium mirabile* Schott. Stamen of male flower.

Fig. 25. *Gorgonidium mirabile* Schott. Male flower from the upper region of the spadix, 7 stamens connate with one another.

Fig. 26. *Stylochiton natalensis* Schott. Inflorescence, enclosed by the lower, tubular part of the spadix; at natural size.

Fig. 27. *Stylochiton natalensis* Schott. Female flower, at high magnification; *a*: seen from above, *b*: from the side, *c*: after removal of half the perigon and a part of the ovary wall, {*d*:} TS through the ovary, *e*: an ovule, more highly magnified.

Fig. 28. *Stylochiton natalensis* Schott. Male flower, *p*: perigone, *g*: rudimentary gynoecium.

Plate III.

Fig. 29. *Arisaema ornatum* Miq. Female inflorescence; the inflorescence axis is slender and covered with thread-like floral rudiments above the the gynoecia which are enclosed by the spathe tube.

- Fig. 30. *Arisaema Dracontium* (L.) Schott. Androgynous spadix. The oblique rows of the male flowers, which are distant from one another, continue into those of the female flowers. Male flowers usually formed from 2 stamens, in *m* and *o* reduced to a single stamen; *n*: a flower in which a staminode is developed in the place of a stamen.
- Fig. 31. *Dracunculus vulgaris* Schott. Half of a TS through the male part of the inflorescence; the individual flowers very unequal; but all formed from 3 more or less developed stamen primordia [Staubblattanlagen].
- Fig. 32. *Dracunculus vulgaris* Schott. Various flowers from the upper region of the male inflorescence, enlarged. *a*: flower with 3 stamens; *b*: a similar flower but in which because of the elongation of the connective, 2 stamens reveal a tendency to become staminodes, *c*: flower with a fertile stamen, a transitional stage to a staminode and a fully formed staminode; *d*: floral rudiment with 3 staminodes.
- Fig. 33. *Helicodiceros muscivorus* (L.) Engl. Part of the inflorescence from the border region. Adjacent to each parastichy of the female flowers is a rudimentary flower (*r*), and after these the male flowers continue in somewhat steeper parastichies.
- Fig. 34. *Helicodiceros muscivorus* (L.) Engl. The same male flowers as shown in Fig. 33, sectioned transversely; it can now be seen more clearly that in the two upper rows each {group of} 4 stamens facing each other belong to one flower, , while the flowers of the lowermost row have developed only 3 stamens.
- Fig. 35. *Arum maculatum* L. Part of the lower male inflorescence with bordering rudimentary flowers. The limits of the individual male flowers are somewhat more strongly marked; the flowers and floral rudiments denoted by the same letter belong to the same parastichy. Two floral receptacles [Höcker] *a* and one floral receptacle *b* have differentiated only two stamens, and the floral receptacle *x* only a single one; on the lower rudimentary floral receptacles we find one or two filaments [Schwänchen].
- Fig. 36. *Sauromatum venosum* Schott. Part of the female inflorescence with bordering floral rudiments which through very strong and thus very unequal elongation are very distorted; the parastichies are nevertheless partly still recognizable.

- Fig. 37. *Sauromatum venosum* Schott. Part of the male inflorescence with the floral rudiments bordering it on the lower side; the male flowers are formed from 2 – 4 sessile stamens, the lowest with only one stamen and running out below into a very elongated receptacle, further down only elongated floral rudiment {occur}.
- Fig. 38. *Cryptocoryne Huegelii* Schott. Male inflorescence greatly magnified. All flowers {are} 2-androus. Drawn by Dr. Pax.
- Fig. 39. *Theriophonum crenatum* Blume. Part of the male inflorescence. All flowers monandrous.
- Fig. 40. *Biarum crispulum* (Schott). Male inflorescence. Flowers somewhat irregularly arranged, the central ones mostly formed from 2 stamens, the lowest *c* with only one stamen; but towards the base running out into a receptacle [Höcker]; also {there is} a monandrous flower above.
- Fig. 41. *Biarum Bovei* Blume. Male inflorescence. Flowers formed from 1 – 3 stamens, but it is difficult to determine, where the flowers are most densely crowded, which belong to a {given} flower. Drawn by Dr. Pax.

Plate IV.

- Fig. 42. *Biarum tenuifolium* Schott. Whole inflorescence except the thread-like appendix, strongly magnified. The parastichies of the flowers can be followed very well up as far as the upper floral rudiments, {but} become very steep between the female and male inflorescences as a consequence of the notable elongation of the floral rudiments which all end in a conical tip. All the male flowers are monandrous.
- Fig. 43. *Pinellia rubifera* Ten. An entire male inflorescence flattened out. The parastichies are difficult to recognize. Each stamen probably represents a flower. The two stamens *l* are partly connate. Similarly the various tritheous stamens are probably the result of connation of two stamens.
- Fig. 44. *Ambrosinia Bassii* L. Spathe seen from the ventral side, showing the female chamber with the single female flower; the male chamber is behind the flattened spadix.
- Fig. 45. *Ambrosinia Bassii* L. Spathe dorsally cut open and opened out so that the male chamber with the male inflorescence is visible.

- Fig. 46. *Ambrosinia Bassii* L. Longitudinal section through the whole inflorescence so that both chambers are visible, *c – c* {position of the} narrow strip on which the lateral expansion [Excrescenz] that joins the spadix to the spathe is formed.
- Fig. 47. *Ambrosinia Bassii* L. Ovule strongly magnified with the conducting trichomes arising from the funicle.
- Fig. 48. *Pistia stratiotes* L. Spathe, partly opened laterally so that the whole inflorescence is visible.
- Fig. 49. *Pistia stratiotes* L. Male inflorescence of the same spadix with the outgrowths situated below it, more strongly magnified. The roof-like outgrowth *c* protects the young stigma, the cup-like outgrowth *b* catches the pollen which falls from the stamens. The male inflorescence here consists of 4 monandrous flowers.
- Fig. 50. *Pistia stratiotes* L. Three different male inflorescences (*a, b, c*) seen from above.
- Fig. 51. *Pistia stratiotes* L. Stamen or male flower in apical view and in TS, strongly magnified. Figs. 48 – 51 by Dr. Pax.
- Fig. 52. *Homalomena rubescens* Kunth. Part of the male inflorescence with 3-, 4- and 5-androus flowers. It can be seen that the 3-androus flowers *a* and *b* are oriented in different ways.
- Fig. 53. *Homalomena rubescens* Kunth. Part of the inflorescence from the border region {between male and female inflorescences}. See text on p. 311. *a*: a larger staminode as found in the staminodial flowers.
- Fig. 54. *Homalomena rubescens* Kunth. {Tangential} section through the part of the inflorescence shown in Fig. 53.
- Fig. 55. *Homalomena rubescens* Kunth. Female flowers with its staminode, lateral view.

Plate V.

- Fig. 56. *Philodendron brevilaminatum* Schott. Part of the female inflorescence with probably abnormal flowers in which individual carpels (*a* and *b*) have formed separate pistils, while the others have grown together into a polymerous pistil (*c*); staminodes present around the gynoecia. After Schott.

- Fig. 57. *Philodendron brevilaminatum* Schott. A flower { similar to those of Fig. 56 }, lateral view.
- Fig. 58. *Schismatoglotiis rupestris* Zoll. et Moritzi. Part of the inflorescence from the border region, strongly magnified. *a*: female flowers without staminodes; *b*: female flowers with 1 – 3 staminodes; *c*: rudimentary flowers with 3 – 4 staminodes; *d*: floral rudiments with only a single staminode; *e*: male flowers each with two staminodes and a stamen; *f*: male flowers with 3 or 4 stamens. Above these flowers the limits between the individual flowers become indistinct.
- Fig. 59. *Dieffenbachia latemaculata* Engl. (or *sp.* ?). Part of the inflorescence from the border region. From *a* to *b* female flowers with very variable number of staminodes, at the bottom 2 flowers that have grown together. *c*: Flowers with more strongly developed broad staminodes and rudimentary gynmoecium; *d*: staminodial flowers with broad, connate staminodes (synandrodium). The other flowers are staminal flowers (synandria). Drawn by Dr Pax.
- Fig. 60. *Gonatanthus sarmentosus* Klotzsch. Female inflorescence with 3 synandrodes at the border, of which *c'* and *c''* still show a central cleft, so that here the staminodes have still not become so completely fused as in *c*. The lower female flowers are sterile, having become pistillodes.
- Fig. 61. *Colocasia Antiquorum* Schott. Part of the female inflorescence with the synandrodes on its border. The parastichies *a* – *e* are very distinct, and also *f* fairly so, but *g* and *h* are indistinct. The structures lacking stigmas in parastichies *a* – *e* and also partly in *f*, are pistillodes.
- Fig. 62. *Xanthosoma helleborifolium* Schott. Small piece of the female inflorescence with the bordering synandria. The two female flowers, *g*, *g* each with a single staminode. The 3 staminodes *x*, *x*, *x* are still not fused into a synandrode.
- Fig. 63. *Ariopsis peltata* Graham. Young inflorescence after removal of half the spathe. The arrangement of the male flowers is clearly displayed in spirals.
- Fig. 64. *Ariopsis peltata* Graham. The same inflorescence in longitudinal section.
- Fig. 65. *Ariopsis peltata* Graham. The same inflorescence in transverse section; *h*: the cavities around which the connate stamens are situated; *o*: the openings {stomia} of the thecae.

Fig. 66. *Ariopsis peltata* Graham. Transverse section of a gynoeceium strongly magnified.

Fig. 67. *Ariopsis peltata* Graham. Transverse section of a synandrium from the lowermost part of the spadix.

Afterword

Until now, I have been unable to find bracteoles [Vorblätter] in any Araceae even as an exceptional occurrence [... auch nur als Ausnahme von der Regel ...]. It is certainly true that I had noticed two spathes on the spadix of *Anthurium Laucheanum* which is cultivated in Borsig's glasshouses in Berlin, of which the second was situated immediately below flowers, and thus had the position of a bracteole [eines Vorblattes]; but this case was not so interesting as the following one. In a very robust spadix of *Anthurium magnificum* in the Kiel botanic garden there were found two 5 – 7 mm long, lanceolate bracteoles in the lower and middle third of the inflorescence. Had these been larger, they would have had the same condition as the bracts that appear in the inflorescence of *Typha*, which have the acquired the function of protecting a complete portion of the inflorescence at the young stage.

SUMMARY TABLES

<i>Lasioideae</i>								
Homochlamydeae hermaphroditae				Achlamydeae unisexuales				
Ovarium	Loc. ∞ - ovul.	2-ovul.	1-ovul.	Loculi 1-ovulati			Amorphophalleae	
pleiomerum			<i>Ophione</i>	<i>Hydrosme</i>	<i>Plesmonium</i>	<i>Synantherias</i>		<i>Amorphophallus</i>
isomer. (2 – 3- locul.)	<i>Urospatha</i> <i>Cyrtosperma</i>		<i>Dracontium</i> <i>Lasia</i>	<i>Hydrosme</i>	<i>Thomsonia</i>			<i>Amorphophallus</i>
oligomer.	<i>Cyrtosperma</i>	<i>Echidnium</i>	<i>Lasia</i> <i>Anaphyllum</i> <i>Podolasia</i>	<i>Pseudodracontium</i> <i>Anchomanes</i>	<i>Nephtytis, Oligogynium, Cercestis,</i> <i>Rhektiphyllum [sic]</i>			Nephtytideae
Lasieae				<i>Montrichardia</i>		Montrichardieae		

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<i>Philodendroideae</i>							
Semen albuminosum						Semen exalbuminosum	
	Stamina libera				Synandria	Synandria	Stamina libera
Ovarium	Placentae						
	parietales	subcentrales	centrales	basales			
pleiomerum	Ovula plura			<i>Thaumatophyllum</i>			
	Ovula 1 – 2			<i>Philodendron</i>	<i>Philodendron</i>		
				<i>Philodendron</i>	<i>Philodendron</i>		
isomerum vel subisomerum	Ovula plura	<i>Schismatoglottis</i>	<i>Homalomena</i>	<i>Chamaecladon</i>			
		<i>Bucephalandra</i>					
		<i>Piptospatha</i>					
		<i>Rhynchophyle</i>			<i>Microcasia</i>		
	Ovula 1 – 2			<i>Zantedeschia</i>			
oligomerum	Ovula plura				<i>Peltandra</i>		
	Ovula 1 – 2			<i>Philonotion</i> (placenta lateral.)	<i>Peltandra</i>		<i>Aglaonema</i>
					<i>Typhonodorum</i>		
	Philodendreae					Aglaonemeae	

No further details are given of the subgroups which can yet be recognized within these.

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<i>Colocasioideae</i>					
Synandria					
	consociata	libera			
Ovarium		Semina albuminosa			Sem. exalbum.
subisomerum	<i>Ariopsis</i>	Plac. basal.	Plac. pariet.	Plac. subcentral.	Plac. central. vel basal.
		<i>Gonatanthus</i>	<i>Steudnera</i>	<i>Chlorospatha</i>	
			<i>Remusatia</i>	<i>Xanthosoma</i>	
		<i>Alocasia</i>	<i>Colocasia</i>	<i>Caladium</i>	
		<i>Schizocasia</i>			
Loc. 2 – 1 –ov.					<i>Porphyrospatha</i>
oligomerum					
pluriovulat.				<i>Caladium</i>	
uniovulat.			<i>?Hapaline</i>		<i>Syngonium</i>
	<i>Ariopseae</i>	<i>Colocasieae</i>		<i>Caladieae</i>	<i>Syngonieae</i>

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<i>Monsteroideae</i>						
	<i>Homochlamydeae (Perigoniatae)</i>			<i>Achlamydeae (Nudiflorae)</i>		
Ovarium	Loculi			Loculi		
	pluriovulati	2-ovulati	1-ovulati	1-ovulati	2-ovulati	pluriovulati
pleiomerum						<i>Anepsias</i>
isomerum	<i>Spathiphyllum</i> <i>Holochlamys</i>	<i>Spathiphyllum</i>	<i>Spathiphyllum</i> (Sect. <i>Amomophyll.</i>)		<i>Monstera</i>	<i>Anepsias</i> <i>Rhodospatha</i> <i>Stenospermation</i> <i>Rhaphidophora</i>
oligomerum				<i>Scindapsus</i> <i>Cuscuaria</i>	<i>Epipremnum</i>	<i>Epipremnum</i>
	<i>Spathiphyllaeae</i>			<i>Monstereae</i>		

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<i>Pothoideae</i>						
	Folia linearia ensiformia	Foliorum petiolus lamina distinctus				
Ovarium	Homochlamydeae hermaphroditae	Homochlamydeae unisexuales	Homochlamydeae hermaphroditae		Achlamydeae hermaphroditae	Achlamydeae unisexuales
			Semen			
			albuminos.	exalbuminos.		
isomerum loculis pluri- vel 2-ovulat.	<i>Acorus</i>		<i>Anthurium</i>	<i>Heteropsis</i>		
		<i>Zamioculcas</i>	<i>Anthurium</i>	<i>Pothos</i>	<i>Amydrium</i>	<i>Culcasia</i>
		<i>Gonatopus</i>				
loculis 1-ovulat.	<i>Gymnostachys</i>			<i>Pothoidium</i> <i>Anadendron</i>		
	<i>Acoreae</i>	<i>Zamioculcaseae</i>	<i>Anthurieae</i>	<i>Pothoeae</i>	<i>Culcasieae</i>	
Oligomerum 1-ovulat.						

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