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MILOŠ DEYL:

VÝVOJ ROSTLIN A SYSTÉM JEDNODĚLOŽNÝCH

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Translated from the Czech by

Julie Moscheles and Greta Hort

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PŘEDMLUVA.

V poslední době se přírodovědci stále více zajímají o vývojové otázky. Je to jeden z nejobtížnějších biologických problémů, jehož správné vyřešení bude mít dalekosáhlý význam nejen pro theorii, ale i pro praxi. Může jím být posílena i naše snaha po získání nových a výkonnějších rostlin, prospěšných lidstvu. Nesprávné představy o vzniku druhů, které v posledních dobách byly velmi silně kritisovány, byly jistě příčinou neúspěchů mnoha pracovníků při pokusech o aplikaci v zemědělství a lesnictví. Všechny nové myšlenky musí být podrobeny důkladnému a methodologicky správnému výzkumu dříve, než se dostanou do praxe. Toto časové zdržení je nutné, neboť jinak by mohly vzniknout značné škody a často i dobré myšlenky by se pak mohly odsoudit zároveň s odvržením nesprávných. Ukvapenost ve vědě, i když spočívá často na nadšení a zaujetí pro nové možnosti, může mít velmi nepříznivé následky hospodářské. Získávání nových vědeckých poznatků postupuje většinou velmi pomalu.

Posledních 100 let ovládala představy přírodovědců Darwinova theorie o vzniku druhů. Během této doby nahromadilo se ohromné množství fakt, která jsou v souhlasu s touto theorií. Jen pomalu se hromadí i fakta, která do této theorie nezapadají a bude nutno revidovat představy o vývoji. Je přirozené, že existence fakt, které nesouhlasí s některou theorií, nemůže popříti fakta, která pro ni svědčí. Je nutno však snažit se je vykládat takovým způsobem, který by dovoloval zahrnout co největší počet fakt a přiléhavěji je vysvětlovat než tomu bylo dosud.

Řadu let jsem se zabýval vývojem rostlin a v tomto pojednání pokouším se řešiti některé problémy poněkud odchylným způsobem než dosud. Zdůrazňuji však, že je to pouze pokus. Při tak obtížných problémech není možno očekávat, že se hned napoprvé podaří naprosto vyhovující závěry. Jedná se mi spíše o upozornění na nové možnosti a jejich prověření odborníky, kteří pracují v tomto oboru. Všechny svoje představy jsem se snažil podepříti fakty. Jedná se o velmi složité problémy, u nichž jistoty nelze dosáhnout, neboť naše znalosti jsou dosud velmi kusé a látka ohromná. Opíral jsem se o vlastní pozorování v přírodě i o údaje jiných odborníků. Největší pomoc jsem však získal studiem rozsáhlých světových sbírek botanického oddělení Národního musea. V našem herbáři jsou bohatě zastoupeny typy skoro všech rodů rostlin, často rostoucí i velmi vzácně v odlehlých částech světa. To mi umožnilo řešit i generelní vývojové otázky. Pozorováním čeledí, rodů a druhů a jejich variability je možno dospět k představě, jak se tyto mění a jaké principy asi ovládaly jejich vznik. Zdá se, že v novější době studium taxonů bylo zaměřeno na přílišné podrobnosti a tím generelní pohled na vývoj se značně zastřel. Tento generelní pohled však se získává jen neustálým srovnáváním bohatých herbářních dokladů. Makromorfologické znaky, snadno viditelné na všech exikátech, jsou jedním z nejcennějších prostředků pro získání všeobecného přehledu. V případech nejistoty je nutno doplnit toto pozorování i znaky anatomickými. Jejich variabilita v rámci velkých taxonů je však dosud málo známá a snadno může dojít k jejímu přehodnocení.

Za hnací sílu evoluce pokládám schopnost hmotných částic neustále se komplikovat a tím nabývat nových a nových vlastností. Tento princip je jednotný od nejjednodušších částic anorganických až k nejvyšším živým celkům. U rostlin dále předpokládám analogický vývoj v ontogenesi jedinců a fylogenesi všech rostlin. Na základě toho jsou pro fylogenesi přiznávány různé fáze s různým významem pro vývoj. U každého taxonu rozeznávám období mladistvé tvárlivosti, jako makroevoluci, a období mužné specialisace, jako meso- a mikroevoluci. Tato období končí stařeckým odumíráním. V prvním období, makroevoluci, jsou možny velké změny a vznik nových taxonů. V druhém nastává dokonalý vývoj orgánů vedoucí především k vysoké specialisaci k prostředí, avšak vyšší taxony se již nevytvářejí. V této práci omezil jsem se jen na proces makroevoluční. Problematika druhů a nižších taxonů, ač je nedělitelnou součástí vývojových představ, bude publikována později. V období makroevolučním nezdá se mi, že by účelnost vystupovala jako charakteristický znak nových taxonů. V práci vyhodnocuji rovněž význam morfologických, anatomických, ekologických znaků pro vývoj a možnosti paleobotaniky i fytogeografie pro evoluční výklady. Všechny tyto kapitoly jsou zaměřeny hlavně k vývoji jednoděložných rostlin, které byly rozděleny na 8 vývojových skupin, taxonomicky odpovídající řádům a charakterisované podobným celkovým vývojovým směrem. Tyto vývojové skupiny se někdy dosti odlišují od doposud uznávaných vyšších taxonů. Rovněž čeledi skládající každou vývojovou skupinu řadím někdy odchylně než dosud a někdy je i nově vymezuji.

Z technických důvodů byl jsem nucen vyrovnat se s mnohými problémy jen velmi stručně a proto je podávám velmi zhuštěně s poměrně málo příklady. Jinak by rozsah byl příliš veliký a možná, že by i základní principy zanikaly ve spoustě fakt. Veliký rozsah byl rovněž příčinou, že práci nebylo možno vytisknouti najednou a byl jsem nucen se omezit jen na procesy makroevoluční.

Je pro mně milou povinností poděkovat za vzorný anglický překlad doc. dr Juli Moschelesové a dr G. Hortové. Této obtížné a namáhavé práce se ujaly s nevšední ochotu a svými bohatými odbornými zkušenostmi mi umožnily někdy i zpřesnit moje představy.

Dosud člověk byl schopen přetvářet jen nejnižší taxonomické jednotky, většinou pouze v rámci druhů. Aby mohl být schopen podstatněji měnit organismy, je nutno zabývat se daleko podrobněji průběhem vývojových procesů. Tím bude snad jednou umožněno daleko převratnější získávání organismů výhodných pro lidstvo než dosud. Jednou z nejdůležitějších podmínek pro to je rozluštění problému vzniku vyšších taxonů a zjištění rozhodujících činitelů při tomto procesu.

INTRODUCTION

Our view of the taxonomy of the plants and of the causes of the origin and development of the species is the outcome of various answers given to the questions involved already centuries ago. The present, quite acceptable conceptions explain most of the problems and phenomena which we observe in nature. And yet much is still unclear, and it is not even probable that we shall be able to clarify it all in the near future owing to our lack of the necessary facts. These will still have to be provided. Already today from the facts at our disposal it is possible to search for and to find a new explanation which will better explain the known facts than the old one, and which will include in a more general scheme of normal causal relations also many of the facts which the old explanation had to regard as exceptions. In the present book I wish to try to solve some evolutionary problems, often perhaps using conceptions which deviate somewhat from those previously employed, but which are based on an analysis of the facts. The problems with which I have to deal are, however, very difficult and subtle, and the feeling for the correctness of a solution cannot be obtained from what we have to admit is after all only fragmentary facts and scattered knowledge. I have tried, however, to harmonise my conceptions with the phenomena observed in nature and to suggest new possibilities of explanation from a wider point of view. Even should my conceptions prove rather simplified, yet by drawing attention to the problems as I see them, I may perhaps awaken the interest of other experts in them, who then may find the correct solution, and it is just this which I regard as the most important contribution which a work of this kind can make to our common fund of knowledge.

The present work will deal briefly with new possible explanations of the course of the evolutionary processes proved so far mainly from the Monocotyledons. Thus it is especially the problems of the higher taxons with which I shall deal here, postponing the questions relating to species till a later date. But the questions of species form an indivisible part of our conception of evolution, and it is on them our conception of the higher taxons rest. I have tried to conceive of the macro-evolutionary development as a unified whole, taking its place in the evolutionary processes of the whole of nature. It goes without saying that it is not the aim of this work to solve all the complex evolutionary problems. But I should be glad if it would further even a little whether directly or indirectly, the discussion of these problems. I am convinced that only by such discussion is it possible to progress towards the most probable solution of this extremely complex and difficult condition for the correct understanding of taxonomic questions.

Basic Conceptions relating to the Evolutionary Processes.

The greatest wonders in nature are the simple, basic particles, from which our whole world is formed. The whole of nature is formed by only a few basic particles, and we do not even know whether these cannot be still further simplified. These particles can, however, form a remarkable number of different combinations. The interaction of these particles results in a great complexity of the substances which have originated from these particles as well as of their properties. On the whole therefore the simple properties of the basic particles give rise under certain circumstances to the formation of substances with more complex properties, which however, are always built only from these basic particles arranged in space according to law. By this the changing outer conditions make possible the assertion of the different properties of matter and of the substances arising from it, by which the basic matter becomes gradually constantly more complex. As an effect of the passage of time it comes to the origin of more and more complex substances.

Another remarkable property of nature is that there is no origin of just any combinations in it, but the origin of certain wholes on the basis of an affinity to combine. The combinations of the basic particles are by no means absolutely free, but show themselves from the very outset bound to wholes which according to law correspond to their properties. In this way electrons, protons, neutrons and other basic particles form certain categories of higher wholes progressing from the atom to the molecule, to compounds, until finally to the most complex wholes known so far—to the living organisms, which just like all of the preceding categories of wholes rise from simple to the most complex ones. Though all these wholes have the same basic material composition, and differ only by the different quantitative arrangement of the basic particles in space, yet they acquire entirely different properties; and with this we have reached one of the greatest mysteries in nature, the interdependence of matter and properties. The reason why it is so extremely difficult to penetrate into this mystery is that we never have an opportunity to study property separated from matter or matter separated from property. Our observation is too imperfect to give us a knowledge of matter without properties and properties without matter. But it is probable that one cannot be known without the other, and that these two categories are always in firm junction. Matter always manifests itself to us only by its properties. The rule applies mostly here that the more complex the whole, the more complex are also its properties.

Another important point with regard to the origin of wholes is given by the conditions under which these can from. Each whole can originate only under certain conditions, which may, however, vary within rather wide limits, and which may also occur in different combinations. Sometimes different conditions may give rise to the same wholes. It is necessary to emphasise the order of importance of the individual causes. Very often the outer conditions are regarded as the decisive agent in the origin of certain wholes. This seems, however, to be incorrect. I shall give quite a simple example to show this: the transition of water into steam under normal conditions takes place intensively at 100^0 C or, as one says, water boils at 100^0 C. Here the condition is therefore a temperature of 100^0 C. When, however, at a constant lower temperature pressure is reduced, boiling occurs at a temperature lower than 100^0 C. Here the condition for boiling is therefore pressure. In both cases there is, however, an indispensable constituent, namely water or the property of a certain inner arrangement of the material particles. It therefore appears to me that this material composition, and therefore this inner agent, is more important than the outer conditions, which may differ.

One of the most important agents of what takes place in nature is besides space also time and the possibility dependent on it of change in space. The natural wholes cannot give rise to the highest wholes and the lowest wholes simultaneously, but mostly the simpler ones arise earlier than the complex ones. The evolution of the wholes is therefore conditioned by time, for it is a basic property of the wholes that they can interact and can form constantly new wholes and often also more complex ones. On the assumption of the existence of time, space, and the capacity of the basic particles to enter into combinations of greater complexity the formation of new wholes with always new properties must take place. On this rests the principle of evolution in nature. This evolution is, however, in the most complex wholes, i. e. in the organisms, irreversible. This is given also by time, which does not flow in all directions, but only in one direction. Reversible evolution may sometimes occur in the simpler, anorganic wholes. The capacity of the basic particles for gradual, more and more complex polymerisation is a fundamental principle of the evolution of nature. This evolution resulted not only in the origin of anorganic nature; the materially same basis with its potentialities made possible also the origin of the far more complex organic nature. Man, however, cannot ever achieve certainty as to whether what actually did happen was the only possible and necessary happening or not. The question is here whether the world could not look different by the assertion of other more combined possibilities or under other conditions. This, however, is a philosophical question, and the biologist is less interested in what might have been than in what is. The purpose of the preceding considerations was to make it clear that evolution is necessary on the assumption of a complication of matter in space, time and quantity, and that the evolution of organic nature is irreversible.

The capacity of the material particles to combine is, however, restricted, and mutual combinations of parts of wholes are not possible, but always only the combination of a complete whole with a complete whole, even though the complete wholes which combine need not be on the same evolutionary level. Another restriction in the combining of wholes is the difference in their capacity to combine. This restriction is fairly great, and thus there arises the enormous simplification of nature, for a vast number of wholes cannot mutually combine into new wholes, as there is not in them the affinity for such combination. We observe another remarkable phenomenon in the stability of the wholes. The wholes formed have mostly a considerable stability in the environment in which they originated, and can be disturbed only with relatively great difficulty also in another environment. This conservatism of the wholes causes also a rather considerable restriction of the properties of combination and stabilises evolution.

With our present knowledge we can on the whole understand well the simple, anorganic wholes and their propertis. It is already far more difficult to understand the higher, organic wholes, in which often properties are formed which are difficult to explain. Nevertheless there is no doubt that they are composed of the same basic particles as the simple anorganic wholes, but they are already so complex that they form mechanically almost ununderstandable units. The fundamental principle is nevertheless simple, and rests on the capacity of some wholes to combine and to form new wholes on a higher level, with far more complex properties and mostly also entirely different from those of the wholes originally fusing.

In what follows I shall deal especially with the origin and evolution of a part of the highest wholes, with the plants. The basic conceptions given above on the evolutionary processes were given in order to explain the basis on which my further work is built.

The Main Evolutionary Factors of the Organisms.

Already the first plants of which traces have been preserved in the earth's crust are extremely complex and have reached a high evolutionary stage. They are already organisms mostly composed of cells. From the origin of life to the origin of the cell many millions of years propably passed, far more, it appears, than from the formation of the first cellular organisms till today. Traces of a precellular life have not been preserved or have not been discovered as yet. Thus we do not know how the organisms formed from anorganic matter, and even if some transitional substances might have been preserved it is difficult to see how they could withstand the attack of present-day organisms, which would certainly use them as a source of nutrition. But even if this were not so, it would still be difficult to find a bit of some plasm which does not multiply much and has only the capacity to accumulate energy and to maintain itself by reactions which proceed very slowly.

Evidence of precellular life and of the way in which living cells were formed from it can be obtained today at best only indirectly. We may assume on the basis of wide experience with present-day organisms that the primitive evolutionary principles appear in the evolutionarily more advanced types. In the evolution of the plants some feature may undergo a great evolution while at the same time another feature is preserved in a primitive state. As there is a great number of evolutionary lines, we can by careful analysis come to know many such rather primitive features, and from them we can form an approximate idea of the probable course of evolution, but we cannot acquire certainty about this unless we succeed experimentally in imitating at least some of these evolutionary principles, and we are still very far from that. Nevertheless in the plants certain processes can be observed which might witness to such primitive evolutionary principles, and which would also show us the way in which it came to the formation of the high wholes with the remarkable properties which we observe today in the organisms which originated from originally anorganic matter.

One of the most important principles seems to be that of the fusion of heterogeneous complex particles into still more complex wholes with many times more complex properties. Traces of such a phenomenon are found throughout the whole evolution of the plants, e. g. in copulation, i. e. in the combining of two bodies for the purpose of forming another organism. Here often a new organism is obtained which stands on a higher level. Another such principle is e. g. the fusion of two representatives of different evolutionary lines, and the formation of a new organism far more capable of surviving in habitats where often neither of the original simple organisms could have lived permanently. An instance of this is the formation of those remarkable living beings the lichens. These cases might be cited in justification of the view of a separate origin of the individual parts of the cell. By the fusion already of these very complex and finished parts a cell might be formed as a new whole at a higher level of evolution. Also the morphogenic effects of viruses, discovered by J. Klášterský in cowl-shaped leaves, give evidence of the fusion of two wholes having the capacity to introduce changes, and indicate far-reaching effects in which it is not excluded that such changes become hereditarily stabilised.

Another important principle might be also the formation of new substances within the organisms, which then are of great importance effecting changes not only in the whole metabolism but also in the shapes of these organisms. In these cases we would then have the interaction of two wholes on different evolutionary levels. Often a great effect may also result from the formation of substances which cause only a different distribution in time of the individual processes taking place in the organisms. It is necessary always to presuppose that each hereditarily stabilised change must be preceded by a certain change in the material composition, or at least in the time-course of the action. It is possible to observe this change of substances in the evolution of the plants, for the lower plants differ often essentially also in the production of some organic compounds. A modification in matter thus plays an important rôle in phylogeny.

The possibility of a mode of life without cells is indicated e. g. by the myxomycetes. Though these are already much advanced evolutionarily, and are very different from anything that existed in the primitive state, yet their mode of life may be very primitive, and may indicate the processes which must have taken place in the far past in the formation of more complex organisms.

A whole number of such fundamental evolutionary principles could certainly be found. They enable us to form at least some idea of how living matter and organisms evolve. It is highly probable that similar ways of material transformation lead always to higher and higher organisms. In fact, so complex do the organisms become, and still more their properties, that we often are at a loss how to give an account of them; such complex, almost ununderstandable phenomena occur in them as occur sometimes also in the far less complex operation of higher mathematics.

Because of the limitation of human knowledge we are forced to take a rather passive part in solving the origin of the evolutionary processes in nature. Our main task is to collect a great number of observations of facts which will exhibit the actual assertion of certain processes in nature. These facts have then to be worked as logically correctly as possible by comparison and generalisations. But even then it is still necessary to control the conclusions resulting from these observations by comparing them with other phenomena in nature. When we find disagreement or new possibilities of interpretation, then the conceptions of the phenomena connected with the evolution of the organisms have to be corrected again, and thus we have gradually to discover the generally valid foundations of the most probable evolutionary theories.

Ontogeny—Phylogeny

Little attention has been given so far to the analogy existing between ontogenetic and phylogenetic evolution. The development of the individual organisms is fairly well known, as are also the processes governing this development, for these processes take place on the whole quickly and repeatedly in a vast number of cases. We can also easily subject the ontogenetic development to experimental investigation. On the other hand phylogenetic evolution takes place on Earth in only one case, for the whole evolution of all that is living is really one process of the living organisms. Nevertheless the two processes show in their foundations very similar evolutionary lines. The development of the individuals takes place in a well defined and united whole, centrally governed by laws, whereas the evolution of all that is living disintegrates into a great number of individuals, apparently without any such central governing and often with indistinct relations in remote lines. Nevertheless it appears that both lines are governed by the same laws, and that both differ only by the different manifestations of the different mode of differentiation of the wholes. In principle, however, both processes rest on the capacity to combine different wholes which have a mutual affinity and relation. In this way a new whole is formed at a higher level with far more complex properties.

We have to regard all that is living as one whole which is subjected to similar laws as the development of each single individual. Thus regarded it is one whole of individualised parts spread into a large space and time in contradistinction to the centrally governed individuals. Thus also new evolutionary possibilities arise, unobservable in the individuals. Thus they are subjected to evolutionary processes, similar to those in the development of the individual; in the origin of any new phylogenetic line there are a stage of youth, a stage of growing and stabilisation, a stage of decline, and finally death. The only difference is that in a centrally governed individual these processe take their course once in the life of the individual, whereas in the evolution of all that has life this evolutionary process repeats itself always with the rise of a higher new whole when new evolutionary possibilities come forward. The cause lies probably in the combining of two wholes, i. e. in our case of the living individual and some newly formed anorganic whole as a new substance, group of substances or new organ, which then changes the whole metabolism of the earlier individual. Every essential change of properties and shapes can be due only to material changes, which precede it. This cyclical rise of the new is, however, not a really cyclical process, as it occurs at always higher and higher levels, and only the basic principles of these processes are analogous.

The development of every organism on the one hand and the evolution of all living things on the other hand appear thus to be characterised to a certain extent by a predisposition given by the potential properties of the matter which forms them. At the beginning of the evolution of all organisms the shape and composition are always entirely different from what necessarily develops from it in their natural aging. Our knowledge of the relation of properties to matter is, however, limited, and with new complications of matter we foresee the properties mostly only when we know already of analogous cases. Even with not living complex organic substances we cannot know beforehand what will arise by the combination of two substances without some previous experience. This is so to an even greater extent with regard to evolutionary processes, as we do not know even perfectly the substances which enter into the evolution, and have to conclude on the basis of analogous cases as to what progressive shape and properties will arise from these substances. Nevertheless shape and properties are always potentially given in the basic material composition. This does not mean of course that this combination can result in only one definite evolution, for under the influence of different conditions this evolution may have the most different manifestations. The reactions, however, to any set of conditions and at any evolutionary level are always given by matter.

The initial stages of the ontogeny and phylogeny of our plants are very similar and consist of simple cells. Never, however, can we tell beforehand what will develop from a given initial stage even though this is already firmly predisposed. In the individual the capacity to develop is circumscribed, and its development proceeds within the limits given by fairly narrow and very sharply defined possibilities of development corresponding to the central governing. But already the first cells included in themselves all the basic principles of possible development, all of which have, however, not been realised. Similarly as in chess it is not possible to bring out all possibilities of the game in one game. But also in this one case the action of time is necessary so that matter may be able to organise and constantly to produce new forms. This gradual organisation is necessary, and we cannot skip some evolutionary stages and thus accelerate the process of evolution. It is only possible sometimes to shorten these stages by favourable conditions, but they can never be omitted.

As the evolutionary lines may be entirely independent of each other, different evolutionary lines are possible in the phylogenetic development. As this evolution takes its course here on Earth only once, we have not even the possibility to foresee where this evolution leads until it has begun to manifest itself. The predisposition of evolution in biology means that the material properties, i. e. the chemical and physical arrangement of the individual particles, involve the necessity of a certain evolution, manifesting itself by characteristic processes. For every evolution certain conditions are of course necessary, which to a certain extent may influence or interrupt it. In ontogeny an example of such an evolution is given by any fertilised egg cell of plants. It is predisposed to form in its evolutionary process again a plant more or less similar to the parents from which it arose. This evolutionary cycle consists under normal conditions always in certain morphological changes and on their basis also in physiological changes which follow on each other according to given laws and which lead to the characteristic formation of the organ and its function. The outer environment may, however, at any time interrupt or somewhat modify such an evolutionary process. I shall return later to this relatively insignificant action of the environment on such modifications.

A similar material predisposition as that which governs the development of the individuals appears to govern also the evolution of all living beings. The evolution here is also possible only within the limits given by the material composition of the organisms. Though the time of the duration of the evolution depends on the outer environment, yet the evolutionary process itself is in the first place governed by the matter of which it is or can be composed. The great difficulty in acquiring any knowledge of the phylogenetic evolution is its uniqueness, in contradistinction to the ontogenetic development which takes its course in many parallel cases. Of course there is the possibility of penetrating the mystery of phylogeny by acquiring a complete knowledge of the evolution which already has occurred, which would enable us to know also the direction which the further evolution would probably take. But this method of penetration will always involve considerable errors of observation and wrong generalisations. We are here faced with a similar dilemma as the historian who studies events which took place only once. Moreover, it is not excluded that something quite new may occur in nature, which again may have surprising consequences. For humanity it is, however, already a great aspiration to desire to know at least roughly the passed evolutionary processes and thus to understand what has happened in nature.

In evolution we observe always two characteristic antithetic processes. In the march of the generations the organisms either change or remain more or less the same. This phenomenon is of the greatest importance for an understanding of the phylogenetic processes. It is only in this way that different phylogenetic stages can maintain themselves side by side, and this enables us then to establish their relations. If an unceasing evolution took place in all organisms, representatives of earlier evolutionary levels could not maintain themselves, and only organisms of approximately the same evolutionary value would exist at any given time. If this were the case we could learn something about their evolution only from imperfect fossil remains. Thanks, however, to the conservative capacity to persist on the same evolutionary level many representatives also of the most primitive groups have been preserved to this day. Thus we have the possibility to compile by means of paleontological data fairly probable evolutionary lines. It is thus the conservatism of the organisms which has caused the present systematic manifoldness.

The phylogenetic evolution is the sequence of qualitatively and quantitatively varying individuals leading to the wealth of forms of different phylogenetic lines. It is dispersed and governed by the material potency of the substances from which the organisms are built. The ontogenetic development is on the contrary a compact development, leading e. g. to the development of the different organs within the centrally governed organisms, such as the development of leaves, roots, etc. This development leads mostly to a greater specialisation and to a greater complexity of the organs. It is natural that when in one organism different evolutionary differentiations may arise in its different parts, differentiation may result all the more easily in a dispersal into independent wholes in different individuals. When it comes to explaining phylogenesis we are in much the same position as an organism with a life-span of one day trying to understand the ontogenetic development of individuals with a life-span of many years. The necessary evolutionary process from the egg through youth, maturity to old age and death would certainly seem incomprehensible and straightout mysterious to it. But something similar happens also to us when we consider the evolution of all living things, which takes place in the world only in one whole. Today, however, already much indirect evidence has been accumulated indicating that this evolution takes place as a whole whose dispersal into different individuals makes the rich complexity of the evolutionary process possible.

Progress and Specialisation.

Two different processes can be distinguished within every evolutionary process in plants, one of progress and one of specialisation. Progress is the process of such changes in the following generations as lead to the origin of new individuals systematically at least equivalent to the parent individuals. It shows itself in great evolutionary vigour, a vigour which may lead later to a rich flourishing. It is a property which we do not recognise from the morphological or physiological properties of the individuals, but only by the observation of many consecutive generations. Such observation is very difficult in living material and often scarcely possible. Therefore we are mostly dependent on the historical reports given by geobotanical or phytogeographical data. Progress corresponds then to the evolutionary stage of youth.

Specialisation is distinguished from progress. It is a process in which types constantly more perfectly adapted to the environment are formed in the successive generations, but mostly with declining evolutionary vigour. They lead to orthogenetic lines in which we observe an increasing strengthening of certain advantageous shapes and properties. Finally, however, adaptation becomes so specific that it may lead to the extinction of types because of their ecological and evolutionary inelasticity. For here only one property is perfected, while others are gradually lost. Specialisation corresponds to the evolutionary stage of maturing and aging of the evolutionary process. When we valuate the time division of progress and specialisation in the individual lines we arrive at the conception of phases of evolution.

Phases of Evolution.

Paleobotany and phytogeography supply much evidence that the evolution of the plants did not proceed uniformly in the course of geological times, but that the individual groups originated rather suddenly. Within a relatively short time a whole number of evolutionary lines originated, which had differently complex structures of their bodies. Mostly we find already very soon side by side representatives with an advanced and with a primitive structure. The gradual origin of types derived from primitive types is thus little probable. Thus it does not come to the formation of more and more advanced types, but we find primitive and advanced types simultaneously side by side. The paleobotanical facts thus contradict the prevailing taxonomic conception as to the gradual origin of more complex taxons from simple taxons, and hence we are forced to seek for another type of interpretation of the evolution of the plants. On the basis of the analogies mentioned above between the periods of phylogeny and ontogeny, and of numerous facts which will be given below, we arrive at the conception of different phases of evolution. In the phylogeny of the plants we can distinguish three such phases.

(1) The euryplastic phase is the phase of evolutionary youth and plasticity. In this evolutionary phase the plants are capable of great changes in all their properties. Here the presuppositions are given for the formation of higher taxons. Often the new forms are not appropriate, as their inappropriateness can be overcome by the great plasticity of the other properties and shapes by which possibly unfavourable outer conditions are overcome. Thus the dominating principle is here not suitable organisation but plasticity in the most diverse directions. It appears that the higher taxons originate in this period as far as to families, and that this period lasts a relatively short time.

(2) The stenoplastic phase is characterised by the stabilisation of the changes achieved in the preceding phase. The plants are still capable of considerable changes. Suitable organisation appears more often. This phase may already be very long, and often maintains the potential capacity through several geological periods. Thus it may have as a result also an increase of the evolutionary potency in later times, which shows itself in the origin of secondary evolutionary centres.

(3) The pseudoplastic phase is characterised by a constant adaptation to the outer environment. Higher taxons mostly do not originate any longer, but only individual organs, and the physiological properties adapt constantly better and better to the outer environment. This phase lasts practically for the whole of the life-time of the lower taxons. At last by the complete loss of plasticity to the environment and often by high specialisation the plants gradually become extinct.

On the basis of these evolutionary processes we can divide the evolution of every large group of plants into three periods according to the predominating phases of the evolutionary processes:

(1) Macro-evolution comprises the processes in the euryplastic phase. It is the evolutionary progress leading to the formation of the mother types of higher taxons with a strong evolutionary vigour, i. e. with the capacity to yield in the offsprings a number of higher and of course also lower taxons. In the evolutionary progress the evolutionary value of the original mother taxons is increased. It is a spontaneous process based presumably on the principle of the complication of the properties of matter under the influence of the affinity of wholes to combine and to form more and more complex properties. This process occurs rarely, and in the evolution of the Earth we know only of a few such macro-evolutionary bursts in the evolutionary potency in plants. The chief agent in macro-evolution seems to be matter complicating itself. Macro-evolution arises by the affinity of wholes which are able to combine and leads to evolutionary progress, i. e. to the origin of types taxonomically mostly higher than were the original individuals, or at least equivalent to them. Usually the foundations of families and higher taxons are laid then. The properties arising in this period are usually not purposive and their maintenance is made possible by the high plasticity of the other properties and characters.

(2) Meso-evolution (I have to thank Academician B. Němec for suggesting this term to me) comprises the processes in the stenoplastic phase. It is the period characterised by the formation of secondary centres of evolution due to the resuscitation of the evolutionary process. This resuscitation may originate by the combination of the material elements given by macro-evolution by their getting into favourable conditions. It leads to the perfection of the properties. Thus taxons originate equivalent to the mother taxon and/or lower ones. Often there appear here already the beginnings of great orthogenetic lines adapted to a certain environment by their morphological structure as well as by their ecological properties.

(3) Micro-evolution comprises the evolutionary processes in the pseudoplastic phase. The adaptation of the plants to different

special habitats already predominates in this period. Most of the morphological and physiological properties formed are expressly purposive, and it is only rarely that indifferent features also arise. Harmful features lead to the doom of their bearers, as they cannot any longer be compensated for by high evolutionary plasticity. Most of the properties become difficult to change, though they are usually not unchangeable. Mostly the newly formed properties do not exceed the circle of the genus, and mostly only deviating species arise. Micro-evolution is a predominantly orthogenetic process, which mostly aims at purposive devices which gradually perfect themselves more and more. This perfection is, however, the result of the intervention of the outer environment in evolution. It leads to an increased ability to survive in the given conditions, but mostly with the loss of other, not indispensable properties. The main agents in micro-evolution are environment, time, and space. They resolve the conflicts between the outer conditions and the inner properties of the plants. Specialisation proceeds also now, and evolutionary weakening leads to inelasticity which though it may persist for long must mostly lead to extinction.

The evolutionary phases are not of course sharply delimited either by evolutionary vigour or by time. Already in the macro-evolutionary period of some of the taxons other taxons passed into the stenoplastic or even pseudoplastic phase, so that they underwent a rapid aging. Such types can only rarely have maintained themselves to this day. The evolutionary vigour thus did not correspond in time in corresponding taxons. Statically, however, these three phases can well be distinguished, as each phase predominated in its own period, on which it imprinted its character.

One force of macro-evolution conditioning the origin of new complex properties of the individuals is the affinity which enables material wholes to combine to wholes of a higher order. Thus it is the material relationship which conditions progress and the formation of something entirely new. On the other hand complexity may also be acquired by conflicts of the material wholes with the surrounding environment. From the point of view of evolutionary progress these properties are, however, not important, as they do not really cause the progress. They only direct the evolutionary progress produced by the macro-evolutionary fusion of materially related wholes into certain lines able to exist in the environment. The conflicts cause the destruction of the multiplication of the wholes which are purposively adapted to the environment. But they do not increase the evolutionary vigour. The latter is given by the material predisposition arising in macro-evolution, or in meso-evolution. As an example may be cited the differentiation of the family *Orchidaceae*. By material affinity there originated here a great number of lower taxons with hereditary stable and often so complex characters that they reduced the chances of persistence. By the action of conflict with the environment such species were furthered in which some purposive device originated which enabled them to overcome the environment better than other taxons. Thus there were formed within this family three different lines defined ecologically: terrestrial, epiphytic and parasitic. Their aspect is very different, but all are clearly connected by macro-evolutionary morphological characters. This purposive device was of great importance for the number of the individual types, but it seems never to have caused evolutionary progress which would have formed some other family. Numerically the types with advantageous properties were more abundant than the types with indifferent characters, as the former had more suitable opportunities to establish themselves. From an evolutionary and taxonomical point of view those types are often more important which preserve themselves only in a few specimens. Adaptation to the environment thus did not cause an evolutionary differentiation, but only a multiplication in nature.

This distinction between the evolutionary processes seems to agree better with the paleobotanical facts, and further elucidates the areas and mutual affinity of all taxons. Thus it is very important also from a systematic point of view. Progress aims mostly at the multiplication of the evolutionary lines, whereas specialisation leads to the directing into one evolutionary line. The higher taxons mostly do not rest on morphological, physiological, etc. characters, but to a far greater extent on the evolutionary potential, i. e. the number of related groups which can arise from a certain type. The morphological and physiological characters are only the secondary consequences of this evolutionary process. In taxonomic valuation we find often a pragmatic evaluation, which often helps us far better to distingunish the importance and height of the individual taxons than the real size of the morphological modification. Therefore taxonomy often valuates what really has vindicated itself in the evolution far more than the real morphological difference, i. e. the degree of organisation of the sex and vegetative organs. There are any number of examples of this. Thus e. g. if in the family *Amaryllidaceae* only one species had developed, it would most probably have been referred to the family *Liliaceae* or *Iridaceae;* or, if the family *Iridaceae* had only one species this would probably have been referred to the family *Amaryllidaceae,* etc. Or again, if some large family as e. g. the *Bromeliaceae, Gramineae, Cyperaceae, Orchidaceae,* etc. were monotypical, their systematic placing would certainly be different. And vice versa, if e. g. around the genus *Streptochaeta* some hundred genera were to form with similar features, they would certainly form an independent family. The same would be the case with the genera *Colchicum, Gagea, Prionium, Cypripedium,* etc. The system of the plants can easily lead to an overestimation of the number of taxons, and thus be laden with pragmatism. The number of taxons is, however, very often the result of the evolutionary potential, and taxonomy must valuate it accordingly. The number of lower taxons is, however, rather the result of ecological adaptation to the environment and expresses often more purposiveness than real evolutionary vigour.

Purposiveness in the Evolution of the Plants.

Very often the view is adopted that the principal agent in nature is the selection of well adapted organisms which more easily survive in the competition for existence than ill-adapted organisms. As not even two organisms are equal, an evolutionary pressure is given by which more and more perfectly adapted organisms are formed. It is assumed that all characters and properties are or at least once were purposive, i. e. advantageous in the struggle for survival. Such a purposiveness strikes one, however, as being rather mechanistically conceived, and evolution is according to this view interpreted only as resulting automatically from it. The evolutionary principles in the plants are, however, far more complicated, and purposive adaptation seems to terminate this evolution and to lead rather to the cessation of evolution than to its unfolding. Further this view does not give an account of the causes of evolution, but only of the way in which it is being directed. But in no case can the exterior technique of the actualisation of evolution be regarded as the cause of the inner evolutionary tendencies. We might with equal justification consider heterogamy to be the cause of evolution, which likewise contributes to the evolutionary manifoldness, but does not cause it. Thus the whole of this problem has to be re-examined on the basis of the facts we find in nature.

The cause of evolution is frequently sought in changes in the early ontogenetic stage or in an accelerated evolution in the individual stages. But even this explanation does not account for the progressive evolutionary complication, which is most marked just in the mature and final stages of ontogenesis. If evolution were advancing towards modifications in the ontogeny, there could never be progress in the final stage, in which evolution always manifests itself the most expressively. In the younger stages it would not lead to the origin of something new, but only to a perfection of the stages already gone through. Also this conception thus does not elucidate the basic evolutionary principles, but at most again only micro-evolutionary changes. The basic evolutionary principles must rest on a material change already from the very first stages until maturity of the individual. After all, the change in the ontogeny is not the cause but only the effect of certain material changes.

One might ask why there is not evolution by regression from what is higher to what is lower. This would appear to be simpler than progressive evolution. On the assumption of a competition for survival or changes in the ontogeny this might often be advantageous. Yet we never observe complete regression. Though we know evolutionary regression which simplifies organisms into more primitive ones as far as morphological structure is concerned, we do not know of any single case in which a more highly organised living being would become more primitively, more lowly organised. Evolution never goes into reverse. If evolution could be explained by evolutionary pressure caused only by the fight for survival, by genetic processes, or by a change in the ontogeny, regressive evolution would occur. Then we should have retrogressive, more and more primitive evolutionary lines. The evolutionary processes known up till now show that evolution is irreversible and does not lead to true primitivity.

The survival of the fittest explains only why some species are more abundant in nature, others more rare or even becoming extinct. But this has nothing to do with evolutionary progress. Evolutionary progress consists in the capacity to produce offspring of another type. The assumption that these successful types have also a stronger evolutionary vigour is not correct, for if so, strongly multiplying types would show a far greater capacity for forming new forms than little numerous types. Thus e. g. annual plants would have to show a far greater number of taxons, i. e. they would have to produce also a far greater number of families and genera than perennial species. These types would have to show far greater evolutionary changes than the ligneous plants and the perennial herbs. This, however, is not so in nature, but on the contrary evolution is usually approximately equal in all. The influence of outer conditions causes only a specialisation in forms, i. e. orthogeny leading to a greater capacity for survival in the descendants. It is a process eliminating from among the descendants all those types which have some properties at variance with the environment in which they live. Therefore such specialised types have great possibility to spread strongly over against badly specialised types.

One might object that such a pressure would act also at the time of strong evolutionary vigour, and that thus there would be already here a furthering and overmultiplication of the types purposively organised. Nevertheless we do not find any evidence of this in the features of the higher taxons, although we might have expected to find it. Most of the characters which taxonomy determines as characters of the higher taxons are indifferent or often even unfavourable from the point of view of purposiveness. It is certain that the sex organs in the *Orchidaceae,* the dioeciousness in some representatives of the *Dioscoraceae,* the bizarre flowers in the *Thismiaceae* cannot be regarded even as indifferent features. Similarly it is difficult to use purposiveness to account for some features of the highest families such as the parallelism of the leaf nerves in most of the Monocotyledons, the concrescence of the petals, the differentiation or non-differentiation into calix and corolla, the enlarged stamens in the family *Tecophilaeaceae,* the abortion of one circle of stamens, the formation of bracts at the base of the flowers of some *Iridaceae,* or the umbel in the *Amaryllidaceae,* the formation of apo- and syncarpous ovaries, the dimerous flowers in the monocotylic *Stenomaceae, Cyclanthaceae, Polygonateae,* the varying number of carpels in the *Centrolepidaceae, Araceae,* the one stamen in the *Zingiberaceae,* the digitately or pinnately divided leaves in the palms, etc. Such examples could be multiplied ad infinitum. In general we may say that most of the taxonomically important features are at least indifferent from the point of view of advantageousness for these groups. From this it necessarily follows that the purposiveness of the features is not the decisive factor which caused the differentiation of the plants into so many diversified types. It is a remarkable circumstance in nature that just these systematically important features become very stabilised notwithstanding their indifferent character, while the advantageous features are easily changed and modified even in the lowest taxons.

Nevertheless it is very remarkable that the great majority of properties and features is purposive and proves useful. Only the conception of an evolution in phases can thus again provide us with an explanation. Essential evolutionary changes are caused as said by the material affinity of matter which enables it to combine, and the result of which is that the properties become more and more complex. This action of mutual affinity does not, however, result in a fortuitous mixture, due only to the laws of predisposition. In nature a whole cannot change just in any way, but only as given by certain factors and in a certain direction. The possibilities are relatively limited, and actually all the various types of changes can be reduced to only a few basic principles. Their combination and the different proportional quantities which enter into it lead, however, to a considerable manifoldness of the resulting forms. An important property of evolution is here that by the influence of the process of metabolism all modifications are harmonised into harmonious wholes. Every change harmonises itself on the one hand by orthogenetic evolution, on the other hand also by phylogenetic evolution. Only rarely do aberrations arise incapable of survival, but if the changes were governed only by combinations according to the law of probability such aberrations would be far more abundant in nature. We must assume that there is in the living organisms a kind of autoregulation of all processes and their integration into a harmonious whole which is mostly able to survive. Everything is connected with and has a complex correlation to everything else in an organism, conditioned of course by matter. Thus when a strong root system develops in a plant there mostly develops by the origin of a surplus of store substances also a strong growth above ground; thus e. g. in the bulbs or in the onions the ontogenetic development may be accelerated and the preconditions may also be formed for large, early spring flowers, as we find it in the bulbous plants. Many a disadvantageous modification can be compensated for by advantageous modifications, e. g. the non-formation of protected winter buds may be compensated for physiologically by the hardiness of the unprotected buds against frost; the difficulty of the fertilisation of some *Orchidaceae* may be compensated for by the long time during which the flowers can be fertilised, a weak generative multiplication may be compensated for by a strong vegetative one, as e. g. in *Lemna, Elodea,* etc.; small flowers by their being crowded together to form a rich inflorescence as in the *Eriocaulaceae, Araceae, Palmae, Cyperaceae, Gramineae,* etc. Such correlation often compensates also for a disadvantage in properties or shapes. Often one finds the purposive features onesidedly emphasised, as in such cases of compensation as those given above they stand out most clearly, while the disadvantageous features are overlooked.

The occurrence and distribution of the purposive properties and features in the plants can be explained well by an evolution in phases. It appears that evolution was very rapid in the macro-evolutionary period. The stabilising and conservative heredity factor was probably far weaker than we observe it today. The descendants were probably not so much like the parents, for the percentage of variability was far greater than in micro-evolution. Thus the descendants gave easily rise to new evolutionary lines. As soon as the offspring became like their parents, the evolutionary vigour decreased and finally ceased. That is why we have so few direct relationships and transitions in the higher taxons and on the whole quite a large number in the lower taxons , where already all the descendants resembled each other more or less. In the macro-evolutionary period indifferent shapes and properties could easily assert themselves. When disadvantageous shapes and properties were counteracted by other and suitable properties or shapes, also the features which were disadvantageous in themselves could assert themselves. In this phase each manifested unfavourable property could namely be counteracted by the strong evolutionary vigour of the plants. In the strongly changing organisms there might always develop a favourable modification, and this compensated for the unfavourable modification. Of course this purposiveness did not exercise any evolutionary pressure, but falls within the sphere of normal variability, for if not unfavourable modifications would necessarily have led sooner or later to the extinction of the plants. Purposiveness was thus on the whole a passive property by which the individuals more capable of survival were selected. In the quick sequence of changing organisms also a number of purposively indifferent features could maintain themselves. In this phase indifferent and purposive features may have appeared in almost equal proportion. Adaptation to the environment in the euryplastic phase could largely have only a passive significance. Though the acting of the evolutionary potencies could change the shapes, yet the evolutionary potency, which is independent of shapes, corresponds always to the evolutionary phase of the types at the time. Let us give an example. If there had been no seas on earth, marine plants could not have arisen. This does not mean, however, that the potencies for the evolution of marine plants would have been changed by this, but only that the potencies did not come into action. If a sea exists, the evolutionary possibilities for the origin of marine plants could assert themselves, if not not. Thus the evolution of plants can be directed by environment, but it cannot be created by environment.

We might gain the impression that evolution in the macro-evolutionary period was considerably limited by the lack of opportunity to assert itself, and that it was considerably different from the true possibilities in an ideal environment, i. e. an environment which would fully utilise all evolutionary potentialities. The actual course of evolution on Earth appears, however, not to be too restricted by the lack of suitable environments, and could on the whole fully unfold itself; for on Earth there is a huge number of habitats, and these offer sufficient possibilities for the assertion of the evolving organisms. A strong evolutionary vigour enables the plants to spread quickly and to overcome the most varied obstacles. As evolutionary vigour is more important than the exterior conditions, the most different lines may develop in a similar way provided that they have the same evolutionary vigour. Probably the taxonomic position of these lines is not of special significance, and the same principles may appear in the most different lines on the basis of a similar evolutionary vigour and similar evolutionary conditions. The evolutionary vigour can act in any conditions, and is only directed to one or the other side according to its affinity. It is possible to compare this to some extent e. g. with the capacity of people to build themselves dwellings. On the whole man finds in every environment sufficient possibilities to apply this capacity, whether he builds his dwelling of stone, wood, brick, snow, loam, etc. Here it does not depend on the outer environment, but on the capacity which can be satisfied in every environment.

A restriction in the evolutionary potency might perhaps occur in a uniform environment, where it would presumably come to evolutionary uniformity. On Earth, however, very diversified environments adjoin and interpenetrate each other. Thus it is possible that the evolutionary potency was directed in the most varied directions and all its possibilities were used. We find, however, one remarkable fact. Those evolutionary lines which had the greatest opportunity to assert themselves in the euryplastic phase are most abundantly developed on Earth, i. e. those which adapted themselves to the environment which was the most common at their time. Thus from an ecological point of view we find that those families are the most richly divided which are adapted to life in warm regions, the probably predominating regions in the macroevolutionary period. We have no families growing only in the cold zone, for at the time of the origin of the families the cold regions were mostly restricted only to the high mountains or to small areas around the poles, certainly little extensive in area. The representatives of the cold zones arose probably from tropical plants, thus later and at a time of lowered evolutionary vigour, and therefore no independent high taxons were formed in them. Among their close relatives we find after all also tropical types. Thus though environment directed evolution, it was not the cause of this evolution. We find its main action in the ecological features, whereas in the morphological features a spontaneous evolution often occurred without any correlation with the environment, and governed often only by the inner properties of the matter from which the organisms were formed. When a plant is in the euryplastic phase, not only adaptation to the most different environments as we find them in its area of distribution can manifest itself in it, but also the development of widely different forms. A proof of this variability cannot of course be given by paleobotanical evidence, as this is fragmentary, and we have probably only very few proofs from the time of new-formation. So far paleobotany has found Angiosperms only as highly advanced plants and obviously in the stage of partial evolutionary stabilisation. We can thus learn only indirectly of the evolutionary potency from the types preserved to this day. Just as the cultivated plants of a certain species may give us an idea of the potency of this species by the number of all cultivated and wild forms of it, so also e. g. the representatives of a family can give us an idea of the original evolutionary potency which manifested itself in the formation of all types of this family. According to their number and to the size of the modifications we can at least approximately judge of the relative age of this family with regard to its evolutionary potency.

The number of plants in the euryplastic phase quickly spread in a uniform environment, and at the margins of this environment encountered a different environment. By its plasticity it could produce often forms which could penetrate also into this different environment. Sometimes this process took place easily, sometimes only with difficulty. This depended probably on the material predisposition of each taxon. Often a series of attempts were formed to conquer the new environment. Such attempts took sometimes place in many basic evolutionary lines and steps, from unicellular plants to the highest plants, but with diverse success. As an example we may take the origin of terrestrial forms from aquatic forms. As on Earth there always encountered each other in the most varied combinations a wet environment, a dry, a cold, a warm, a nourishing, a non-nourishing one, etc., the possibilities were given for every large group to form types adapted to these environments. As the pressure to conquer the different environments was present in the higher plants in many lines, and some conquered these environments already in the euryplastic phase and others only in the steno- or pseudoplastic phase, we find today already many related groups or individual species and genera adapted to the most diverse environments.

It seems very probable that purposiveness is not the moving factor in evolution, but only an accompanying phenomenon indicating it. As detrimental properties necessarily lead sooner or later to the extinction of the types characterised by them, there must thus occur a relative multiplication of the advantageous and also indifferent properties in the remaining evolutionary lines. As, however, the carriers of the advantageous properties are especially favourably assisted in life, there will finally be a far greater multiplication of the individuals with advantageous properties than of individuals with only indifferent properties. This is the reason why the purposiveness of most of the features stands out so strikingly in a survey of the present long-time evolution of the forms. Purposiveness arose, however, mostly passively by directed evolution and certainly cannot be used as evidence for the evolutionary processes having been actively assisted by this pressure. Purposiveness causes the multiplication of the individuals with advantageous properties, but not their evolutionary vigour.

One may ask why the cryptogams were not victorious over the phanerogams. The cause certainly does not lie only in the better ability of the seeds to resist the environment. We see that also the cryptogams adapt themselves to very extreme habitats. Thus the *Notholena, Ceterach,* most of the lichens, etc. can grow also as extreme xerophytes. To elucidate this problem we must steep ourselves in the period when each of these groups was in the period of new-formation, and judge of the conditions of habitat, competition, etc. at that time. Conditions were certainly different in every period of the new-formation of great groups, especially the biological conditions. New-formation turned on the capacity to get to a different habitat. Habitats already inhabited had of course to be conquered in a more subtle manner than more or less unoccupied habitats. Better properties had to be developed than those possessed by the old inhabitants, whose imperfections were thus utilised.

The old settlers, who had their period of new-formation already long behind them, could no longer adapt themselves so well. This was useful to the plants which were in the phase of new-formation, and which thus were on a higher evolutionary level. Just this evolutionary vigour led to their victory over types which no longer could adapt themselves so well. The older types did not necessarily become extinct; but they became mostly very decimated, and confined themselves only to a restricted part of all the ecological possibilities.

So far we have discussed the conception of the evolutionary processes in relation to purposiveness within the macro-evolutionary phase. The meso- and micro-evolutionary phases were far more favourable for the origin of purposive forms. In these phases we meet already with clear orthogenetic processes directed towards the constant perfecting of the forms and their specialisation. Meso-evolution is a period of considerable evolutionary capacity leading often to secondary centres of evolutionary bursts. It is probable that these are due to a more suitable organisation of the building elements which arose in macro-evolution, and whose organisation demanded a certain time before its effects could be felt. As the length of this time differed in different representatives, these processes arose over a long period and in different places. They conditioned first and foremost secondary evolutionary centres in plants, on the scale of families as well as of genera. The beginnings of the orthogenetic series might fall in this phase leading to the rich unfolding of some types especially well adapted to special habitats, e. g. desert, cold, aquatic habitats etc. In this phase the lowering of evolutionary vigour made it no longer possible for the plants to react to unfavourable properties by a strong evolutionary vigour which would counteract them. Therefore such unfavourable modifications were mostly doomed to perish, and only modifications with a directed perfection of the properties and advancing specialisation were maintained and determined the trend of the development. But here again we must point out that this does not mean that the pressure exerted by the environment was the cause of the evolution, but only that the environment directed the evolution. In meso-evolution indifferent features still maintained themselves and also arose, though to a far less extent than in macro-evolution.

Very different conditions exist in the micro-evolutionary phase, as we can clearly see in the present plant world. Here specialisation already predominates, i. e. purposive changes leading to a better adaptation to a new environment. The evolutionary potency already recedes, but the plasticity may nevertheless be considerable. This plasticity arises probably by the organisation of the basic elements formed in macro-evolution, and we have here only modifications and nothing essentially new. It appears that this specialisation is characterised by the loss of properties. All the properties and also the material composition corresponding to them interact directly or indirectly. The gradual loss of certain properties, which restrict the perfect development of other properties corresponding to the full utilisation of the possibilities materially given, may result in an orthogenetic evolution towards a onedirectional strengthening of a certain advantageous property, of course at the expense of the whole plasticity. Thus micro-evolution is governed by proceeding specialisation which in some cases is of such a character as to make the plants unplastical though highly adaptable to certain special conditions. Therefore they may perish even with small changes of these conditions, and this leads to the rapid extinction of such species. The micro-evolutionary processes refer chiefly to the questions and conditions within the species, and they will be dealt with in the continuation of this work. Many questions are, however, important for an understanding of the whole evolutionary process, and thus they have to be dealt with, however briefly, also in connection with the questions of purposiveness in nature.

Evolutionary potency and outer environment, therefore the properties of living and non-living nature, are linked together in a harmonious equilibrium. The appearance of any new property of a living organism must cause a disturbance of the equilibrium, and this has an influence not only on the habitat but also on the other organisms in it. Hence it will come to the stabilisation of a new equilibrium different from the original equilibrium according to the magnitude of the change. A harmonious equilibrium is of course not a state of inertia, but on the contrary a rather tempestuous process, which involves considerable changes in the environment, so considerable changes in fact that it is not possible to give a simple account of all the processes which take place.

In the processes which take place in anorganic nature there is usually some correlation between two changes of which one is the cause of the other; if the change which acts as cause is slight so will the change which it causes be, and vice versa. In living nature, however, there is no such correlation, and this makes it exceedingly difficult to grasp clearly what happens here; the interrelations become too complicated. Man, who desires to understand everything, then seeks for a simplified expression which will account for the very complex phenomena he observes, and to this end he forms generalisations and then attempts to account for many, if not all, of the complex interrelations by his one generalised observation. As an example of this we may cite the conception of purposiveness. Purposiveness, as we have shown above, is one, and by no means one of the major factors in evolution, and yet it has been made to serve as the explanation of the whole of evolution. However, man is also a ceaseless enquirer after truth, and as more and more facts become known, as man's knowledge is enlarged, the false or facile generalisations become recognised as such, and corrected.

One of the most interesting properties of nature is its self-regulation, manifesting itself in what is sometimes called the balance of nature. (Balance, however, seems a rather unfortunate term, as it either suggests a state of rest, which we never find in nature, or an unstable equilibrium, which may at any moment result in catastrophe, and this again cannot be said to be an adequate description of the facts as we observe them in nature.) The property of self-regulation appears to be based on the property of matter to form different complex wholes and on its property to fill space, as expressed from of old in the observation "nature abhors a vacuum". The living organisms try everywhere to fill the space accessible to them. By the interaction of the various properties of the lower anorganic wholes and of the higher organic wholes our world arises as a very stable combination under certain conditions. As conditions and properties constantly change complete inertia never occurs. Instead we find here self-regulation: when some organism disappears its place is automatically filled by another organism, and thus a though changed, yet stable combination is formed again.

To account for this property of self-regulation, or rather for the "balance of nature", the conception of purposiveness has again been pressed into service, and moreover in a form which often is thoroughly anthropomorphic, or based exclusively on the most striking and obvious cases observed. In many cases, however, we find that the property which is thus chosen as an example of purposiveness so far from being so is disadvantageous, and that actually it is its opposite property which is purposive. Purposiveness, we may say, has its obverse side. Whether a property is advantageous or disadvantageous is frequently, perhaps always, dependent on the given conditions. When conditions change a property which was advantageous under the old conditions may become disadvantageous in the new conditions. Thus it is very difficult to judge whether any given property is advantageous or disadvantageous: beautiful and well developed seeds become more easily food for birds than bad seeds. Similarly a well developed tree is more likely to be felled by man than a crooked or stunted tree. The greater the sociability of the trees, the easier a parasite can spread epidemically and decimate the stand. In such cases a property normally regarded as advantageous will become disadvantageous and might lead to the preservation of imperfect specimens. Thus it depends partly on circumstances whether one or the other property proves advantageous or disadvantageous. Given an unchanging environment the formation of advantageous properties certainly assists the individual. But with a constantly changing environment they may have the opposite effect. A plant perfectly adapted to an aquatic environment alone has certainly an advantage when living in that environment; but when the place dries out such a plant must perish.

In evolution everything does not depend only on the properties of the individuals themselves, but also on the properties of other organisms and of the environment, and it is then these properties which determine whether certain individuals shall live or not. Even a very imperfect creature may have an expectancy of a long life when its mode of life does not clash with that of other species. In contradistinction to this a habitat densely populated by many types makes usually for a great complexity and specialisation of the types. Often the formation of the most complicated devices which we know today in plants proved unsuccessful in some other evolutionary lines, although in these lines the device in question reached the same morphological complexity. Thus for instance we see that the plants which achieved angiospermy were not always the most successful types and some of them became extinct relatively early *(Lepidocarpaceae, Caytoniaceae)*. Evolutionary complexity is thus not everywhere equally advantageous. The time of the greatest competition among the plants coincides frequently with the time of youth of the individual types. This period cannot, however, exert any very great influence on what the features will be in the mature types, as the features due to the evolutionary progress do not usually begin to appear until maturity.

It is of course a rule that the more complex the structure of the individuals the greater is their capacity of adaptation and the easier they adapt to the most different outer conditions. But we find also many exceptions to this rule as e. g. in the most primitive organisms, among which there occur types excellently adapted to a certain environment. Thus the bacteria, the algae, the fungi are so well adapted to certain habitats that no later, more perfect group could drive them out of these habitats. Thus these types, though they are the oldest on Earth, have maintained themselves permanently. Though they are best adapted to a certain habitat, yet they do not develop further into higher forms. Their evolutionary progress is terminated, and there remains only plasticity leading to more perfect specialisation within a certain environment.

Macro-evolution is followed by meso- and micro-evolution, and these cause constant changes, which, however, are due mostly only to ecological and morphological plasticity within the species or at most perhaps within the genera. When this plasticity ceases to exist, the whole organism must perish sooner or later. It would, however, be incorrect to assume that all later progressive changes are far more perfect than the changes in the preceding periods of evolution. On each evolutionary level, from the most primitive to the most complex, extremely purposive properties arise, not surpassed on the evolutionarily higher levels. Moreover, it is just these properties which cause many representatives of passed periods to survive and easily to hold their own also when growing together with organisms which are for the rest evolutionarily more complex. Thus e. g. one species of bacteria can perform such remarkable processes as even species formed later cannot perform. Also some higher plants such as horsetails, *Lycopodium*, and mosses have very many properties which are so advantageous in certain habitats as to be unsurpassable in these habitats so that these plants can here compete even with phanerogam plants.

In nature we do not find only one species adapted to a certain habitat, but usually a whole number of species. If purposiveness were the overruling factor in evolution, then there would be a tendency towards simplification, and each habitat would exhibit mostly only one species, but that would be the one best adapted to that particular habitat. As it is, we find that some habitats have an extraordinarily diversified flora, consisting largely of types belonging to different groups of plants which have had a different time of their evolutionary climax period. This circumstance should by itself be sufficient to warn us against using purposiveness as the main explanation of evolution.

We speak of purposiveness and of purposive orthogeny mostly only after the event. Often it is very difficult to ascertain the true cause of the happening in nature. Thus e. g. it is an open question whether the narrowness of their leaves made it possible for the grasses to grow in dense stands, or whether the growth of the grasses in dense stands was conducive to the origin of narrow leaves. Often there need not even be any direct correlation between features which at first sight seem to stand in causative relation to each other, but some features may be caused by another, independent agent. Thus e. g. the two features mentioned above may have been caused by material predisposition, and need not be causally related at all, in which case the purposiveness is only apparent not real. Often many disadvantageous and indifferent properties become in the course of evolution purposive, and vice versa many of the purposive properties gradually disappear. In nature the predominance of purposive features was often brought about by the relative restriction of types with detrimental features, and thus it came to the multiplication of types with purposive features. Often, however, the differences in the properties of species are so small that it is difficult to regard them as differences caused by a selection which meant life or death to the species. Thus many species differ only by morphological characters of which it cannot be said that they would be advantageous, and hence many features which we regard today as clearly indicative of purposiveness need not prove so after an analysis of the facts. They seem to be indispensable for evolution, but in fact, though they accompany constantly certain groups, they are not the one necessary condition for the evolution of that group. Often evolutionary differentiation could take its course also without these devices and proceed by forming other devices. Thus e. g. there need not be any causal connection between the alternation of generations and the conquest of dry land by the plants, as is often maintained. There is no reason why the plants could not grow on land without this device. They might have adapted their organs to growth on dry land by simple, either morphological or ecological modifications. Among the lower plants we have many such adaptations, e. g. in the lichens, the dry-loving fungi, and the algae. We know also of rather large algae *(Nematophythales)* which adapted themselves to dryer habitats. Though they were not successful, yet there is no reason why success should be excluded. Neither is there any reason why the higher plants could not have built their bodies from plectenchyme. The differentiation of the bodies might have proceeded in many other, very different ways, which could have been far simpler and at the same time resulted in perfect ability to continue to live. We have become far too accustomed to regard purposiveness from the point of view of the end results which we see, but we must never forget that these end results are the outcome of one way of evolution, not of all possible ways of evolution. Nor must we forget that as all properties and all shapes acquired through evolution have a certain meaning or function, they will appear purposive to us. Meaningless, fortuitous features cannot and do not exist in nature, as everything in nature is connected with everything else, and each thing has to find its place as a member of the whole. But there is a difference between the mere having a meaning and being purposive. The former term includes a wide range of possibilities, the latter is narrowly defined necessity.

In this connection let us consider the evolution of the Angiosperms. Some botanists trace the success of the Angiosperms to the origin of a covered ovary protected from the outer environment, while others link it up with the origin of a secondary endosperm, and again others with the origin and flourishing of birds and insects. However, there is no direct correlation to be found in any of the three cases, nor is it necessary to seek for any far-fetched explanation to account for the success of the Angiosperms, the only essential condition for their success being given by the great plasticity which this group had, and which enabled it to react to all the possibilities offered it by the then existing, already less plastic plants to penetrate into the places where they were weak. These older types were already evolutionarily stabilised and could not withstand the assault of the new plastic types. It is, however, probable that if e. g. the new-formation had occurred earlier in the Angiosperms than in the Gymnosperms, so that the new-formation of the Gymnosperms would have occurred when the Angiosperms were already stabilised, the Gymnosperms would have ousted the Angiosperms, and not vice versa.

We have thus arrived at the conclusion that purposiveness did not provide the evolutionary pressure which led to the differentiation of the plants. This was most probably provided by the material relations, i. e. the affinity between different organic and anorganic wholes to combine and to form a more complex matter, and in consequence also enormously complex properties. The non-purposive features, which mostly became important taxonomic characters, especially in the higher taxons, prove that as far as the higher taxons are concerned purposiveness played on the whole a small rôle in their origin. The disadvantageous characters were compensated for by the high plasticity of the types which enabled them to adapt to the most different environments. In the species and in the lower taxons on the contrary the predominant characters are purposive, and here, in micro-evolution, purposiveness is thus of considerable importance, as the indifferent and disadvantageous characters cannot be compensated for by an all-sided plasticity as in the macro-evolutionary period.

Morphology.

For the characterisation of the taxons we do not know of any better features than the morphological ones. But even these features do not afford absolutely unequivocal evidence. The basic principles of morphological changes are relatively simple. Only a few basic qualitative types of changes of organs or of their parts are known as e. g. reduction, concrescence, change of symmetry, etc. The combination and different magnitude of these changes may lead of course to an enormous mass of modifications. But each of these modifications can have only a very limited importance for taxonomy. From the species to the families and higher the differential features are constantly of the same morphological quality, and we cannot declare some of these changes characteristic only for certain taxons. Whether something is a character of a higher or a lower taxon is mostly decided by a whole complex of characters and not by one character. Thus e. g. in the Monocotyledons the dimerous or tetramerous flowers which in *Gagea bohemica* constitute a small modification (Velenovský) constitute in *Majanthemum bifolium* a specific character, in the genus *Anthurium* a generic character, and in the family *Potamogetonaceae* a character of the family. Or the ovary of one carpel is a character of the family in the *Gramineae, Cyperaceae,* a generic character in the *Najas, Lilaea,* a specific character in *Amorphophallus sparsiflorus.* A great number of such examples could be given.

Nevertheless it is possible to find characters which clearly indicate relationship. They are extreme characters which occur in the evolution of the plants only once or twice, and then only in very distant lines. A character which occurs more frequently in different lines cannot serve by itself as a weighty distinguishing feature. A character which occurs only once or only very rarely in the evolution of the plants and proves hereditarily very constant in all descendants can on the contrary serve as an important criterion of all taxons characterised by it. Such features may be e. g. the pollinia in the *Orchidaceae,* the spikelets in the *Gramineae,* the carinate bracts below the flowers of some genera of the family *Iridaceae,* the phylocladia in the *Ruscaceae,* the asymmetrical flowers in the *Zingiberaceae,* the utricles in the genus *Carex,* etc. Of course even so no absolute certainty can be obtained, and it is always necessary to pay regard also to the other characters and properties. Nevertheless for determining the relationships the morphological and also the anatomical characters are the most important ones, and it is on them that the whole system is based. It is certain that the evolutionary potency shows itself just by changing these characters, and that the evolution of the plants cannot be imagined without morphological and anatomical changes. Such changes are thus the necessary precondition for evolution.

To gain a correct conception of evolution it is, however, not sufficient to know only the results of the evolutionary processes, one must have also a correct knowledge of the whole phylogenetic process. For this purpose it appears, however, that morphology by itself does not give the possibility of a correct solution of the problem. Much valuable work has already been done by comparative morphology, and it has also been used profusely in taxonomy. Its results are that one has on the whole well defined lower taxons up to the genera and sometimes to the families. The methods of classical comparative morphology are, however, of relatively little use when it comes to constructing the higher taxons, as the relationships here often become unclear because of numerous exceptions and parallel evolution. The data are of far greater use given indirectly by paleobotany and phytogeography or directly by genetics and experimental morphology, as they show the actual course of the evolutionary processes, and it is therefore necessary to evaluate the morphological characters also in the light of the evidence provided by these subjects. When we do so, it becomes clear that comparative morphology has divided the plant body into too independent organs and frequently does not take into consideration the plant as a whole. This whole has a high self-regulating capacity and forms the organs so that this whole may be preserved. This applies equally to the root, the leaf, or the stem. A plant forms one whole, and what morphology treats as discrete parts are not so but on the contrary members of the one whole, and as such interconnected in the most complex way. The weakness of the morphological point of view in which the individual organs are treated in isolation, forcibly torn from each other, shows itself especially clearly when it comes to evaluating the higher taxons. The overestimation of the importance of the details often obscures the importance of the individual features in the whole.

Discussion of the nature of the stamens, ovary, calix, corolla, etc. contributes very little to the solution of taxonomic problems. We see with what ease the plants form these organs and change them, of course within certain limits. Thus e. g. from a simple flower there easily arises an inflorescence as we know it in the perfoliated capitulum of *Bellis perennis*, etc., where each flower of the capitulum changes into a new whole capitulum, etc. It is possible to observe changes also when the metabolism has been disturbed by wounding, chemical substances, or extreme physical interferences. Though these are mostly changes hereditarily not transferrable, yet they show how such changes could arise in the euryplastic phase, and, due to inner material factors, become hereditarily stable features as soon as that which caused these changes in a labile evolutionary balance, i. e. during a high evolutionary potency, became hereditarily stabilised. As an example may be given some results published by F. E. Clements—E. V. Martin—F. L. Longen. When the sprouts were cut off except for two segments in *Frasera speciosa* these lower segments grew flowers which were, however, strongly modified. Either they became considerably longer, or their whole structure was disturbed. Often one or more stamens carried petaloid appendages or sometimes the sprouts became much shorter. When the buds were then removed except for the two youngest ones, the flowers formed either normally, or some became dimerous or trimerous, and often the individual parts changed in size as well as in shape. In other plants, e. g. *Thalictrum sparsiflorum,* the ovaries did not develop in the flowers after compression of the stem so that the supply of nutritive substances was reduced. The injection of honey or dextrose in *Salvia grandiflora* led to a reduction of the corolla and to sterility or a least a stunting of the stamens. The same interference in *Oenothera biennis* caused cleistogamy. Similarly changes in the symmetry and concrescence of the flower parts were achieved by rich nutrition. These examples indicate how relatively easily features might arise which are sometimes highly evaluated in taxonomy as e. g. a modification of the flower plan, the origin of unisexuality, concrescence of the corolla, etc. Also these cases show that we must not regard a change of the structure of the plants from too static a point of view when we wish to discover the causes of these changes and their true significance in the plant as a whole.

It is a question whether the causes of the changes in the structure of the body of the plant are not far more important for an understanding of the evolutionary function of some metamorphosed organs than the final results produced by these causes, i. e. the shape of the organs and their parts. It is possible that different causes give rise to the same shapes, while one and the same cause may result in the formation of different shapes in different parts of the plant. In any case it would be more desirable to explain the organs according to the causes than according to shape. It would be desirable to aim at ascertaining the causality in morphology, for every change of shape must be caused by a change of the material composition or of the sequence of the metabolic processes. It would be desirable to know whether the formation of bulbs is not due to the action of one or several constant material factors which, however, can form differently in different parts of the plant. Similar questions are raised by all metamorphoses. If an experimental trend could be introduced in morphological investigations more light might be thrown on the problems of the material predisposition of certain forms, and this would be of inestimable value for an understanding of evolution, the roads it takes, and thus for achieving a greater certainty as to the relationship of the higher taxons.

Comparative morphology has brought us much evidence concerning the independent development of the organs or tissues, a development which can easily be accounted for by material predisposition. Thus in the Angiosperms the superior or inferior ovaries arise in the most widely different evolutionary lines just as do symmetrical flowers, succulent shapes, anemophily or entomophily, different types of inflorescence, etc. Thus material predisposition is a phenomenon which we encounter very frequently in evolution. For material predisposition speak many facts relating to specially functioning organs developed from different parts of the plants, as for instance the formation of the nectaria in Monocotyledons, as reported by Tachtadžan. The nectar is secreted by nectaries which form in different parts of the flowers, thus e. g. in the genera *Colchicum* and *Smilax* the nectaries are situated in the filaments of the stamens, in *Fritillaria, Iris, Uvularia* in the various parts of the perigonium, in the *Amaryllidaceae* in the dissepimenta of the ovaries in the places where the neighbouring carpels have not completely grown together. This type is the most frequent one in the Monocotyledons. A far more varied picture is given by the Dicotyledons. Thus we have to assume that it is the material predisposition which is decisive for the origin of the nectaries. The material predisposition may assert itself in the most widely different parts of the flowers. From an evolutionary point of view it is important in this connection whether the organ is prior to its function, or vice versa whether the predisposition to a function forms the conditions for the origin of the organs exercising that function. We can observe something similar also in the origin of the roots, which can form anywhere in the plant. Also tissue cultures often show a strong regenerative capacity and often form a bud and from it a new plant.

Anatomy.

The valuation of the anatomical structure of the plants has also contributed considerably to the clarification of some taxonomic problems. Especially a whole number of recent works on the anatomy of plants show an appreciation of taxonomy on the one hand with a confirmation of the results of comparative morphology, and on the other hand it opens up quite new possibilities of explaining relationsphips, and finally it provides a better interpretation of the present classification. Thus the discovery of the alternation of haplo- and diplophases in the life of the organism, further the different mode of fertilisation in Angiosperms and Gymnosperms, the distinction between perisperm and endosperm, etc. have all exercised a great influence on taxonomy. Anatomy brings also excellent evidence for the material predisposition of the different tissues. Thus it has ascertained tracheae in *Pteridium latiusculum,* in the genus *Selaginella,* in the roots of *Athyrium filix femina,* in *Gnetum* and in the Angiosperms. This independent origin can be explained only by the predisposition of the living matter to develop certain forms. Similarly a secondary thickening arises independently in different evolutionary lines.

Anatomical research on the mode of fertilisation has increased the difference between Gymnosperms and Angiosperms. On the other hand the great difference between the naked ovules of the Gymnosperms and the ovary of the Angiosperms was reduced by the discovery of hollow styles in the genera *Butomopsis, Lilium,* etc., in which the pollen can penetrate to the ovules themselves. The protection of the ovules in the ovary thus does not seem to be a device causing the flourishing of the Angiosperms, but rather only a secondary consequence of a complication in the structure of the plant bodies as in other lower angiospermic types. By the study of the ontogenetic development anatomy has contributed also to the distinction of the organs or their parts according to probable affinity. Cytological investigations, too, contribute not only to genetics but also by their interpretation to the taxonomy of the plants. A knowledge of ontogeny and cytology is, however, important first and foremost for the elucidation of micro-evolution. Ontogenetic changes cannot contribute to evolution anything essential that had not already been in it, and thus these changes are probably not of great importance for macro-evolution, but only for meso- and micro-evolution.

Recently also polynology has had considerable success in explaining relationships. But even here the differences in the structure of the pollen do not provide an unequivocal criterion. Mostly they contribute to increasing the certainty of valution as to whether a macro-morphological shape is or is not alien to the group to which it is attributed. Thus polynological investigation has proved useful in taxons of problematic affinity. But the taxons are not characterised by only one type of pollen; sometimes we find also in obviously related taxons several fundamental types. Also the fixation of the shape of the pollen took place in different evolutionary periods, chiefly in meso-evolution, as it is rather constant in the genera, and can here be a good systematic help. Thus C. Mez used this character for the characterisation of the genera of the family *Bromeliaceae*. Here the character of the pollen varies considerably. There are here genera without pores *(Bromelia, Cryptanthus,* etc.), with one pore *(Aregelia, Nidularium,* etc.), with two pores *(Ananas, Quesnelia,* etc.), with two to four pores *(Hohenbergia, Aechmea),* with two to many pores *(Canistrum, Portea),* and finally most often with one sulcus *(Billbergia, Pitcairnia, Puya, Dyckia, Thecophyllum, Catopsis, Tillandsia, Guzmannia, Sodiroa).* For the definition of this family as well as of many others this character is of very little use.

Anatomy gives mostly similar results as morphology; but as it is more difficult to obtain these results anatomically, the anatomical analysis is used mostly for the solution of special problems about which comparative morphology fails to obtain sufficient certainty. Especially where in the evolution of the taxons the anatomical characters became sharply defined anatomy is very useful and often indispensable for taxonomic work. For the higher taxons anatomy has, however, only a limited importance, as already the families, and still far more the higher taxons, are mostly not only anatomically but also morphologically logically heterogeneous. Here the great variability of the characters already comes to the fore, for a considerable uniformity of characters never indicates a high taxonomic value of the taxons. In the highest taxons many evolutionary tendencies assert themselves with variously stabilised characters in the individual higher taxons. Thus on the whole anatomy does not give taxonomy qualitatively new possibilities, but it enables the morphological observations to be made far more accurately.

The study of the relation of the chemical composition of the plants to their taxonomy is only in its beginning. Certain relations are clear, but by and large they are not so easily determined as for the morphological characters. Because of their relative simplicity the same chemical substances may obviously be formed more easily in different evolutionary lines than the causally far more complicated morphological shapes. Nevertheless with the more complicated compounds as with the alkaloids, etc. a certain chemical composition can sometimes define also certain evolutionary lines. When thus the position of any given plants is controversial, the chemical composition can contribute to their correct placing. Perhaps we may expect far more from this investigation when the dynamics and causes of the formation of these compounds will be known. It is, however, exceedingly different to trace the individual reactions and their complex correlations, and it is not made easier by its having to be done by two different workers, by a biochemist and a systematician. It is very difficult for one person to master both of these complex subjects. The chemical compounds which are most easily traced are those secreted in crystals or definite forms in the cells. Also these substances are used for the characterisation of taxons.

Ecology.

The importance of ecology for evolution has often been overestimated. The suitability of an adaptation to a certain environment is not the governing factor in evolution, but only the condition for the multiplication of suitable types over against unsuitable types. Hence physiological properties are frequently not much emphasised in taxonomy. Nevertheless we find that many physiological properties are characteristic for certain taxons, and thus they may be used as a supplement to the morphological characters.

In the evolution of the plants the physiological properties mostly do not maintain evolutionary independence. We do not know of one case in which it would be possible to define higher taxons by physiological properties alone. On the contrary we know many cases in which the physiological properties are almost the same, but the morphological properties not. In the Monocotyledons we have thus e. g. the genus *Potamogeton* and also some others. It appears that morphological types of the same shape, e. g. the individual egotypes of a certain species, can differ ecologically only within the range of certain taxons. It is difficult to imagine different evolutionary lines which would not be characterised by morphological features. It appears that a basic change of metabolism is always connected with morphological changes, and that physiological changes alone cannot on the whole lead evolutionarily to the formation of any essential changes. There appears to be a direct correlation between essential changes in metabolism and morphological changes. Often we find in different evolutionary lines a similar morphological configuration connected with a similar ecology. This is particularly striking e. g. in *Equisetum arvense* and *Tussilago farfara*, where the system of rootstocks and the whole life of the two types strikingly agree. It is also an example of how restricted the possibilities given by predisposition are in the evolution of the plants. The physiological properties consist, just like the morphological features, only of a few basic types, which constantly assert themselves in different combinations. On the whole we may therefore say that the physiological properties are of little importance for the definition of the taxons, though their importance for evolution may be considerable.

At the time of macro-evolution the morphological characters and physiological properties were extremely plastic. But while the assertion of the physiological properties depended on the environment, the morphological characters could change without any influence being exerted by the environment and sometimes only under the pressure of the evolutionary potency. Thus we find often a striking agreement between the ecological properties in different evolutionary lines. In a homogeneous habitat a whole number of very different types of plants could develop; thus e. g. from among the Monocotyledons *Hydrocharitaceae, Aponogetonaceae, Zosteraceae, Potamogetonaceae, Ruppiaceae, Zannichelliaceae, Najadaceae, Lemnaceae, Mayacaceae,* etc. Even in a homogeneous habitat we find a greater number of types living side by side than would correspond to mere purposiveness under the influence of the varying conditions. For the development of physiological properties, however, the possibility to live in a certain environment was always needed. When therefore certain types of habitats were abundant in the euryplastic phase, there were also rich evolutionary possibilities for different evolutionary lines to occupy such habitats. Thus the most abundantly represented evolutionary lines in such habitats will be those in which the physiological properties corresponding to these habitats predominated at the time of new-formation. As the evolutionary potency gradually declines it will be these properties which become fixed most abundantly as constant ones. Thus we may expect that in the higher taxons those ecological types will be represented most which were adapted to the types of habitats predominating at the time of their euryplastic phase. This means that the greater the number of taxons and the higher they are which we find in a certain, ecologically defined region, the more probable it is that this habitat corresponds to the predominating type of habitats at the time of new-formation. This is of course only a rough estimate, as later unfavourable conditions may have changed the picture completely. Yet it may serve as an indication of the ecological conditions in different evolutionary phases. As all families of the Angiosperms have tropical and subtropical types but only some families have types of the temperate zone, it is obvious that the macro-evolution of the Angiosperms took place mainly in a tropical climate. The types growing in a cool area may have arisen either by having preserved their plasticity until the time of the later cooling of the climate, or they may have originated in a tropical climate, but on high mountains, where however lack of space did not permit such a strong differentiation as in species of more extensive habitats. This explains why the temperate zone does not exhibit so great a number of different types as the tropics, in spite of the fact that the habitats in the temperate zone are often still more diverse than in the tropics.

Similarly it appears that the original types of plants were predominantly aquatic to mesophile, for in most of the xerophytes the first leaves are mesophile, which indicates their original character. Dry habitats were presumably rare at the time of new-formation, or adaptation to them was so difficult that it came only slowly and often only at a time when the evolutionary vigour had already decreased.

There is a direct correlation between advantageous ecological properties and the number of individuals of each type. There are as many individuals of each species as there are accessible opportunities. Often, however, a very small number of invididuals is sufficient for the maintenance of the species, but they must have the possibility of maintaining themselves constantly in the habitat. This is the reason why some species do not become extinct although the number of individuals is insignificant.

The formation of new types is, however, far greater in small isolated colonies. The smaller the number of specimens of one species the greater the probability that a modification once formed will maintain and perpetuate itself. In a great number of perfectly adapted types it will on the contrary disappear by back-crossing.

The development of the ecological properties is most often directed towards a greater specialisation for certain habitats. With this is given also the limit of this development. Special adaptation leads to ecological inelasticity, and thus finally even a slight change of the conditions to which these types are adapted will destroy them. Thus specialisation does not lead to the development but on the contrary to the extinction of types.

The history of the types of today provides us with numerous examples of the unchangeableness of the ecological character of some types growing in different conditions. Here we have especially the cosmopolitan weeds. Such types spread over the whole world in countless individuals and enter the most varied environments. In these environments, however, they often do not change much either ecologically or morphologically. This shows that the ecological properties of the habitat have a very small influence on the origin of new types from the types which enter it in the period of micro-evolution. At the same time one and the same species which hardly changes at all in a new environment may be most variable in the region of its original occurrence. In this region more plastic forms of the earlier stage, from the time of maximum plasticity of the species, may have preserved themselves. This indicates the importance of the centre of origin of each type for its evolution.

In the ecological properties we observe two types of adaptation. On the one hand the more primitive capacity of living within a wide range of ecological conditions stabilises itself, and on the other hand the more derived capacity to specialise directly for life in quite definite conditions. Though the first type of adaptation predominates in all species in the euryplastic phase, it is only in some species that this ecological euryplasticity has become fixed and has maintained itself till today. An example from our flora is afforded by the types, here of course at most from the stenoplastic phase, which grow equally well in the alpine zone and in the plain, in sunny and shady habitats, as *Sesleria calcaria, Biscutella laevigata, Saxifraga aizoon,* etc. As an example of the second type of adaptation may be given the absolute adaptation to a certain environment as found e. g. in the strictly aquatic plants, the halophytes, the plants on serpentines, desert plants, etc.

It is interesting to note that in many families and also in higher taxons sometimes all members are clearly characterised by some ecological properties. Here the type obviously arose in a homogeneous environment, where it became so stabilised that it characterises still today the whole evolutionary group as e. g. the *Helobiae, Pontederiaceae, Lemnaceae, Zingiberaceae, Palmae, etc.* All are restricted only to one definite environment.

Paleobotany.

Paleobotany, dealing with the study of plants and their life in past times, has contributed much to the construction of the systems of the vascular plants. It corrected, and certainly will still correct, much in the systems constructed only on recent plants. Any system in fundamental disagreement with paleontological facts is of doubtful value. The paleobotanical data are, however, very far from complete. Only an insignificant part of the types of past times have been preserved, and of them again only an insignificant part has been discovered and worked by the paleobotanists. This circumstance, and at the same time the difficulty of getting detailed knowledge of the events which formerly took place in the formation of the taxons, constitute certainly a grave obstacle to the construction of systems only on a paleobotanical basis. On the other hand the relatively small amount of material preserved makes it easier to gain a general view of the whole system and evolution of the plants and saves us from being swamped by details. The paucity of the material forces the paleobotanists to think more deeply so as to be able to use to the utmost the scanty material they have. Therefore we have, especially recently, so many important paleobotanical contributions to the solution of purely taxonomic questions, especially of the Pteridophytes and Gymnosperms. On the contrary the very many works on the taxonomy of recent plants force the systematician to engage predominantly in description, as the abundance of material often precludes a clear survey of relations, and this state of affairs is still further aggravated by many transition types; thus it is by no means easy to establish the correct affinity of present-day plants. After all, also the paleobotanists find similar difficulties with types which have been preserved in an abundant number. Thus relatively little has been done up till now for the taxonomy of the Angiosperms, whose evolution took place in relatively recent times, and where fossils have been preserved in so great a number that the clear evolutionary lines are obscured. Nevertheless much knowledge can be obtained from the paleobotanical facts for the construction of the system of the Angiosperms, whether from their fossilised remains or from analogy with the other plants. Of the paleobotanical data the following ones are the most important for the construction of systems:

(1) Most of the present types of plants had in their history a time of origin, flourishing, and, except for the Angiosperms, also a time of decline. Thus the plants do not originate uniformly at all times; their occurrence follows well-defined laws in their evolution, which have to be respected also in taxonomy. The evolutionary vigour changes during the evolution of the types, and it is not one and the same thing whether the taxons originate in the early time of evolutionary vigour, or in the time of flourishing, or finally in the time of retreat; we must also ask what kinds of taxons are formed in each of these phases. It is just on these foundations that the conceptions of the phase development of the plants have been worked out.

Paleobotany supplies the best proofs for the sudden appearance of certain basic evolutionary lines and their rapid initial disintegration into higher taxons. In the Angiosperms it encounters even the oldest representatives of these plants on the whole highly advanced and in many basic lines. Mostly, however, we have here only ligneous types, which are most easily fossilised, whereas herbaceous types are often lacking or are restricted to the representatives of swampy or aquatic habitats. The herbs of dry habitats, which do not shed their leaves, are usually not preserved as fossils, and their absence may thus be only apparent. But already in the Cretaceous we find Monocotyledons and Dicotyledons side by side. The Monocotyledons are relatively scarce, but as they are mostly herbaceaus types this is not strange. We find here the *Palmae, Gramineae, Cyperaceae, Araceae,* and of genera *Typha, Sagittaria, Potamogeton,* etc. Of the Dicotyledons we find representatives of the families *Nymphaeaceae, Ebenaceae, Amentiferae, Menispermaceae, Magnoliaceae, Cercidiphyllaceae, Lauraceae, Sterculiaceae, Tiliaceae, Moraceae, Euphorbiaceae, Rosaceae, Leguminosae, Hamamelidaceae, Platanaceae, Ulmaceae, Ramnaceae, Sapindaceae, Aceraceae, Araliaceae, Cornaceae.* Of present genera there are here e. g. the genera *Populus, Platanus, Quercus, Laurus, Liriodendron, Sassafras, Magnolia, Diospyrus, Eucalyptus, Juglans, Tilia, Ficus, Ulmus, Artocarpus, Liquinambar, Zizyphus, Paliurus,* etc. All these are mostly representatives of ligneous types, and we might therefore gain the impression that these types are the most primitive ones. As, however, the herbaceous types are preserved only to a small extent, and as their phytogeographical distribution shows that they have a similar type of area as the ligneous types, we must assume that the herbaceous types were represented here too, but have not been preserved. From the list of the families given it will be seen that they are types which taxonomy places to the primitive types as well as to the derivated ones. Thus the current view that they have arisen gradually by a long evolution will have to be abandoned. The paleobotanical data show that evolution was very turbulent at first, then it took form and shape, and gradually grew calmer until it finally died down. The conception of macro-, meso- and micro-evolution is thus supported by the paleobotanical data. Hence it will be necessary to change the representation used up till now of evolution as of a tree of life, as will be shown below.

The find of extinct groups is also of exceptional importance for taxonomy, as it enables us to gain a more accurate view of the evolution of the organisms. In the Angiosperms it is important that the extinct representatives older than the Miocene cannot be placed today more accurately than in genera. The Miocene and younger types can on the contrary sometimes be identified with species living today. Also this fact supports the conception of varying evolutionary vigour, for species with a great plasticity could not maintain themselves long. The oldest species known up till now is the gymnosperm *Ginkgo biloba,* presumably of Jurassic age. The climax of this group was earlier than the Angiosperms, and it stabilised itself far earlier. If evolution had proceeded at the same rate at all times there would probably be more types which maintained themselves also from the oldest times.

(2) The second paleobotanical discovery which is important for our view of evolution is that each great group observed by itself gradually complicates itself in its structure from its beginning. On the other hand some fossil types show sometimes a perfectly developed structure of

the reproductive or vegetative organs, and these types became extinct relatively soon; the types related to them which have maintained themselves to this day are primitive in comparison with them. Again we see here that extreme specialisation led mostly to a loss of plasticity, and as the specialised types could not any longer adapt to the changing conditions of the environment they died out. Mostly the highest evolutionary stages were connected with complete or almost complete extinction of the types. As an example of this we may give the Lycopsids, in which organs similar to seeds were developed *(Lepidocarpaceae),* or sturdy trunks with a secondary thickening and large roots *(Sigillaria, Lepidodendron,* etc.), and the Sphenopsids in which sturdy ligneous types with a complex structure of the fruit branchlets were prominent; almost all these advanced types perished, and only herbaceous types survived such as *Lycopodium* and *Equisetum,* which are far more primitive; even the origin of bisexual flowers reminiscent of the flowers of the Angiosperms in the *Cycadeoidea* did not save this group from becoming extinct, while again the more primitive Cycases survived. From among the Pteropsida the simpler Pteridophytes survived and the far more highly organised seed types of the *Pteridospermae* became extinct. These and many other examples show that evolution is not directed by purposiveness; on the contrary, it moves towards greater complexity and finally to extinction. Mostly only the more primitive side-lines have survived, in which a concatenation of circumstances led to the formation of a device of special value for survival; but evolution then did not continue any further and remained at the stage reached. Advantageous adaptation may thus lead to a longevity of the types, and sometimes to a great numerical representation of the types, but it is not the driving force of evolution. If the evolution of the plants were guided only by purposiveness there would necessarily originate types so perfectly purposive in the final lines that they would oust all other types from certain habitats and be completely predominant in these habitats. As, however, purposiveness is only a secondary evolutionary manifestation, complete predominance does not occur anywhere and there remains always sufficient room for less perfect types.

(3) The third paleobotanical discovery which is important for our view of evolution is that there existed also in the distant past types of plants which although they belonged to entirely unrelated lines had analogously developed organs. It is just paleobotany which gives us examples of a corresponding evolution in different lines tending to form similar organs. They are examples of the material predisposition of the living matter resulting in parallel evolutionary lines. From a simple and often dissimilar foundation in the initial stage there is here a similar differentiation of some organs in the final evolutionary stages. Such a long-time parallel evolution leaves, however, always features distinguishing the similar final members from each other. This parallel evolution cannot be explained by fortuitous agents, but only by the action of material predisposition of the living matter. If evolution could proceed in any direction from the initial stage, it could never come to such striking phenomena. The clearest evidence of such a parallel evolution

is given by very distantly related lines. Naturally it appears far more often in more closely related lines, where it may often lead to an incorrect estimation of the relationship, the parallel lines being regarded as closely related, although they are not really so. The best known example of material predisposition in the plants is the evolution leading to the origin of seeds and formations similar to seeds. We find these seeds and seed-like formations in the final stages of such very different lines as the *Lepidocarpaceae, Caytoniaceae, Cheirolepidaceae,* and *Angiospermae.* Thus the formation of seeds is not a criterion of relationship. The angiospermy in the higher plants does not appear from this point of view to be the cause of the flourishing of this group, but only an accompanying feature. The cause of their flourishing and predominance on Earth lies rather in their evolutionary vigour than in the ecological significance of the covered ovule. Even if most of these plants had uncovered ovules they could still reach the same flourishing, as we can tell from e. g. the genus *Reseda,* in which the uncovered ovules are not to the detriment of the ecological properties. Another example of this is afforded by the independent formation of secondary wood which occurs in all evolutionary higher plants, similarly as the occurrence of noded axes. A very instructive example of parallel evolution is afforded by the evolutionary lines discovered by Florin, leading to the families *Taxaxeae* and *Abietaceae.* Both separate out very early, and we can trace them already soon almost from the complex of the *Psilophytales.* Via a series of different evolutionary stages they became very similar to each other in the vegetative parts in their final members *Taxus* and *Abies.* The differences in the reproductive organs and the presence or absence of resin-ducts distinguish, however, the two evolutionary lines. If we did not know the evolution they have undergone, we might easily be misled to underestimate these features.

(4) Paleobotany brings us further important data concerning the relations of geological changes to the origin of new evolutionary lines. The assumption that the environment exercises an evolutionary pressure leads necessarily to the conclusion that the great changes of the surface of the Earth and of its climate must be closely related to the origin of new evolutionary possibilities in the plants. The origin of new evolutionary lines should therefore be closely connected with great geological and climatological changes. Such a correlation is, however, not simple. The two processes, though influencing each other, are independent. It appears that the changes in the Earth's crust have no direct connection with the origin of new evolutionary possibilities for the organisms. The geological changes and the changes of climate are, however, directly connected with changes in the habitats. This causes a quantitative re-grouping of the plants, as different types are thus furthered or impeded, and either multiply or perish. The evolutionary processes are, however, influenced by these changes only in accordance with the evolutionary phase in which the plants are at the time of the change. The course of the evolutionary phases has, however, mostly no relation to the geological changes. The geological changes act mostly only as an agent strongly assisting specialisation but not the evolutionary process.

An example of such a course of evolution is given just by the Angiosperms. The greatest progress in their evolution took place in the Cretaceous, which was the period of greatest quietness in the revolutions of the Earth's crust. During the very turbulent Tertiary period, on the contrary, a change in floristic composition occurred frequently, but no higher taxons originated than in the Cretaceous. The Ice Ages brought with them enormous climatic changes and movements of the vegetation, but brought hardly anything evolutionarily new. The multiplication of variability in these ages is only apparent, for with climatic and edaphic changes other types must of course be furthered than those which previously had been so. The types which now got advantageous conditions recruited themselves most probably from among the mountain types, where because of the great wealth of different habitats the most widely different egotypes cou'd grow. They were types until then mostly rare, which paleobotany has little chance to discover as fossils. Thus their arrival in the extensive habitats of the plains after the destruction of the original flora strikes us as the birth of completely new types. But they are mostly types from families known and at most the genera are different.

Paleobotany like all other branches of botany is, however, not immune from making incorrect deductions, all the less so because of the paucity of the material. One of the most important discoveries for the taxonomy of the Angiosperms would be the discovery of the precursors of the group of plants from which they originated. But these are not as yet known, and the question is solved by conjecture. The most diverse groups are regarded as possible ancestors, but with all of them there remains a great gap between the Angiosperms and the group suggested as ancestor, and hence systematics can contribute only little to the correct solution of this problem. Like all other sciences so also paleobotany makes use of hypotheses, of which the most important for taxonomy are the ones relating to the origin and evolution of the different organs. Thus paleobotany has contributed much to the solution of taxonomic questions concerning the vascular plants. But with regard to the Angiosperms it has not as yet proved very successful. The huge wealth of recent types suggests that the present vegetation wou'd form a better approach to the question of the ancestors of the Angiosperms than that afforded by paleobotany.

In conclusion we may summarise the contribution which paleobotany makes to our subject: It provides us with evidence for the age and historical evolution of the plants, for the tempestuous evolution in the early stage, the later rich complexity, and finally, after the formation of very complex types, the dying down of the evolutionary vigour. Moreover, the paleobotanical data, as little as the other data with which we had to deal in the previous chapter, lead to the conclusion that advantageous changes can be the cause of evolution. On the contrary, the data obtained by paleobotany exhibit in a clear form the principle of material predisposition and the parallel evolution of different evolutionary lines caused by it.

Phytogeography.

The huge areas of most of the families of the Angiosperms constitute a remarkable phenomenon which, however, is not fully utilised for the elucidation of the origin of these plants. The family is really the highest taxon which we are able to distinguish rather well by means of the morphological characters and which, when correctly defined, has a monophyletic origin. This can be assumed for most families. As in the course of geological times the distribution of lands and seas changed, and as most taxons of terrestrial plants can spread only on dry land or across narrow marine straits, all continents in which we find the same taxons must have been connected in some way at the time of their spread, and the areas of each taxon which spread on land must therefore reflect the changes between land and sea which took place in the territory of its distribution. Hence if the current view of the evolution of the families is correct, the areas of the families which according to this view are younger and derived from the so-called primitive families will reflect only the younger changes in the distribution of dry land, while the areas of the so-called primitive families will reflect also the older changes. But this is by no means what we find. The areas of the so-called primitive families and the areas of the so-called derivative families do not show any such differentiation according to he differences in time of the paleogeographic changes. The *Orchidaceae, Gramineae, Musaceae, Zingiberaceae* and others have the same area as the *Juncagineae, Hydrocharitaceae, Potamogetonaceae,* or as the *Liliaceae, Juncaceae , Iridaceae, Araceae, Palmae, Commelinaceae,* etc. The families which have small areas and are on the whole rare belong taxonomically mostly to rather isolated types such as the *Thurniaceae, Cyclanthaceae, Mayacaceae, Rapateaceae, Velloziaceae, Roxburghiaceae, Philydraceae,* etc. They have often a very disjunctive distribution, which indicates the great age of these types.

If families originated successively one from the other in the course of geological ages, then those families which originated after the interruption of certain continental bridges, e. g. since the Cretaceous period, must show this in their areal distribution, as each family can spread only in a connected area. But also among the so-called derivative families we find types with disjunctive areas as well as types with connected areas. Thus the phytogeography of the families contradicts the current views of the evolution of one family from the other. This means that we have to realise that our current views of the primitivity and derivation of the individual types are not necessarily correct, but on he contrary are in need of revision, and that we must recast our conceptions so that they are able to include also the distribution of the families. The conception of an eruptive and almost simultaneous origin of most of the families agrees with the facts given by phytogeography. As the families according to this conception originated almost simultaneously, they must have also a similar history of their areas. The size of the area differs mostly according to the ecological plasticity of the individual types. Of some families we can assume that they will have smaller areas because of their low ecological adaptability or excessive specialisation. But the number of these families is very small. Already this indicates the predominance of great evolutionary vigour in most families. This also agrees with the conception put forward above of the almost simultaneous flourishing of the Angiosperms.

Among the Monocotyledons we find in the families almost the same types of areas as in the families of the Dicotyledons. Already this phenomenon indicates that the development of both groups went by similar roads, and their evolutionary centres will correspond to each other. It is also probable that both groups originated at about the same time, as the contrary would have to show in different types of areas of the Dicotyledons and of the Monocotyledons. The older group would show indications of an older distribution of continents and bridges or barriers of distribution than the younger group. As the types of the areas are the same, this can be explained by the same time of origin of both groups.

For the solution of the question of the evolutionary centre of the Angiosperms and of the basic processes in the evolution of this group it is very important that all families have their representatives in the tropics and to a small extent in the temperate zone. The regions in which we find the greatest number of representatives of the higher groups are most probably the regions from which the individual evolutionary lines diverged. This assertion has been criticised because relict species and the possibility of secondary centres obscure the true picture. In making generalisations we have necessarily to reckon with this. On the assumption of a relatively recent eruptive, later more or less declining evolution of the Angiosperms, and when taking into account the great number of taxons, it appears, however, that these influences will most often manifest hemselves as modifying ones, but in the main not conceal the chief evolutionary tendencies. From this point of view the only region which can come into consideration for the origin of the Angiosperms are the tropical lands. This is on the whole natural, for at the time when the Angiosperms originated, whether in the Cretaceous, in the Jurassic, or still earlier, a warm climate reigned on most of the Earth. If new centres had originated in the temperate zone, this would probably show in an excentric distribution of the major number of families, and their distribution would not be almost symmetrically in both hemispheres. But the temperate zone has no family at all restricted only to this zone. Though in the subtropics there occur 17 quite small families of the 303 families of phanerogamous plants, it is not excluded that they are the rests of former tropical types which only later migrated into the subtropics. They consist in seven isolated families in South Africa *(Grubbiaceae, Bruniaceae, Geissolomataceae, Roridulaceae, Achariaceae, Penaeaceae, Heteropyxidaceae)*, one in East Asia *(Eucomiaceae)*, five in Australia *(Corynocarpaceae, Eupomatiaceae, Tremandraceae, Cephalotaceae, Akaniaceae)*, and four in South America *(Myzodendraceae, Gomortegaceae, Aextoxicaceae, Lactoridaceae)*. It is interesting to note that not one monocotyledon family is among them, as all of the monocotyledon families have at least some representatives in tropical regions.

Tab. I. Representation of Families according to Climatic Zones

Climatic Zone	Arctic	Temperate north of 40° N. lat.	Northern subtropical (40—23·5° N.lat.)	Tropical	Southern subtropical (40—23.5° S. lat.)	Temperate south of 50°S.lat.	Antarctic
Number of Families in each zone	75	128	234	275	245	107	2
Number of Families not occurring in the individual zones	228	175	69	28	58	196	301

The above table shows that the greatest number of families is accumulated in the tropics, and that in the direction towards the poles their number gradually diminishes. But this diminishing is symmetrical in both hemispheres. This indicates an origin of the Angiosperms in the tropics, for otherwise it would certainly have come to an excentric grouping of the families with regard to the tropics. The small number of antarctic families is due to the lack of suitable land masses in this zone.

No family is restricted to the temperate zone alone. All extratropical families—27 families in all—reach with their area also into the subtropical zone. The taxonomic position of many of them is not clear at all, and some authors do not recognise them as separate families. Eight families are monotypical, represented by only one species. The others have mostly only one genus with a few species. All are small families distinguished by some characteristic morphological features from the related types. The taxonomic valence of these differences can, however, easily be overestimated. Some of these families may be only extreme types of other families.

Most probably the extratropical families are families which, though they originated in the tropics, later became extinct in them. This is indicated by the area of the families *Hippuridaceae, Sparganiaceae* and *Empetraceae,* which are distributed in both extratropical zones. Of the other families the *Adoxaceae* are restricted to the northern temperate zone, the *Eucomiaceae* and *Cercidiphyllaceae* to Asia, the *Crossomataceae, Leitneriaceae, Limnanthaceae* to North America, the *Phrymacae* and *Cynocrambaceae* to North America and Asia. To extratropical South America are restricted the *Myzodendraceae, Gomortegaceae, Aextoxicaceae, Lactoridaceae,* to Australia the *Akaniaceae, Cephalotaceae, Tremandraceae, Corynocarpaceae, Eucryphiaceae,* to Africa the *Grubbiaceae, Bruniaceae, Roridulaceae, Achariaceae, Geissolomataceae, Penaeaceae* and *Heteropyxidaceae.* For the reasons given above all these extratropical families cannot be taken as disproving that the Angiosperms originated in tropical regions.

Table II. **Classification of the Families according to the Size of their Area**

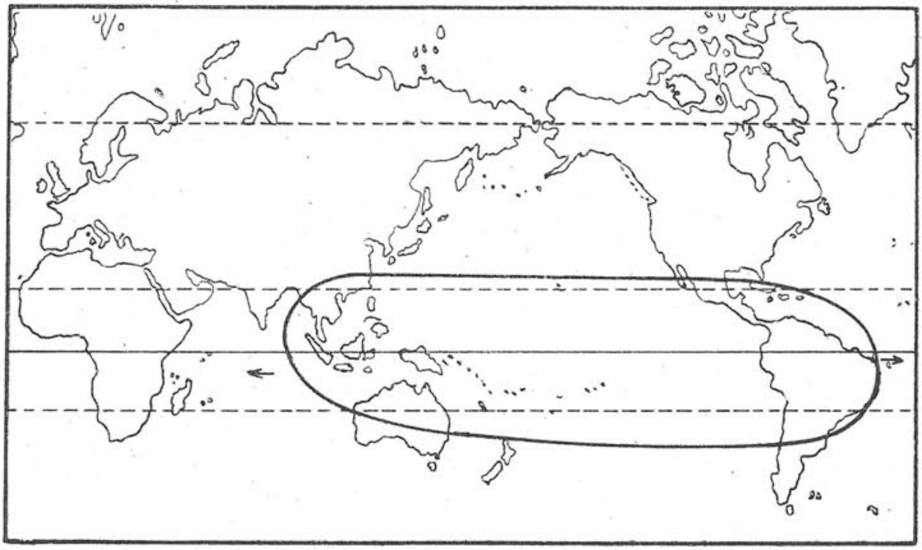
Type of Area:	Cosmopolitan zonal (4—5 continents)	Cosmopolitan interrupted (4—5 continents)	In 2—3 continents	Endemic restricted to 1 cont.	Total number
Number of families:	113	57	60	73	303

When we compare the areas of all Angiosperms given in the above Table it is striking that of 303 families 113 are distributed in a continuous zone around the globe and 57 have a more or less discontinuous distribution but reach on the whole into all tropical continents. There are all in all 73 endemic families. Fossils of some of these from former geological times are, however, known also from other continents. The families with a world-wide distribution can help little towards answering the question of the origin of the Angiosperms. Only the endemic families and those avoiding some continents are suitable for this purpose.

Table III. **Representation of Endemitic Families and of Families avoiding Certain Continents**

Continents:	America	Africa	Australia	Asia	Europe
Number of endemitic families in the individual continents	32	19	14	8	0
Number of families avoiding certain continents	59	87	117	74	174
Number of endemic families avoiding certain continents	42	55	60	65	73
Number of non-endemitic families avoiding certain continents	17	32	57	9	101

The above table shows that Asia has the smallest number of endemic families, and that the smallest number of non-endemic families avoid this continent. This indicates relatively good migration possibilities of this space. Australia has relatively many endemic families, but there are also 57 non-endemic families which avoid this continent. This is probably due to the short time of connection of Australia with other continents at the time of the new-formation of the families, followed by the isolation of Australia, so that other families could not reach it. Also the small size of the continent certainly exercised an influence on the number of families, as it was unfavourable for the maintenance of a great number of types. The American space has the greatest number of endemic species, and a relatively small number of non-endemic types avoid this space. This indicates the proximity of this continent to the centre of the origin of the Angiosperms. The large area of this continent was, however, favourable for the maintenance of many types. Also the north-south mountains made it possible for the cool-loving types to migrate across the tropical region. Africa has a rather large number of small endemic families, and a rather great number of non-endemic families avoids this space. Here, too, there seems to have been a connection at the time of the new-formation of families, but its later interruption prevented many families from reaching this space. Europe lies obviously outside the region in which the origin of the families took place.



Map. 1. — Probable centre of origin of the Angiosperms (indicated by an ellipse).

If the above reasoning is correct, then the centre of evolution of the Angiosperms must be placed in the space of the Pacific, roughly in the region delimited by South and Middle America on one side and East Asia and Australia on the other side (map I). We must of course assume that this space had at the time of the origin of the families to the east and west a connection with Africa. This connection was, however, severed rather early, first on the side of South America and then also on the side of Africa.

The centre of origin of the Angiosperms at which we have arrived is not reached by the areas of 31 families. These are, however, families which, except for 19 African families, occur near the centre of evolution. Of the nineteen African families ten families are not always recognised as separater families at all, and the remaining families are mostly monogeneric. Their occurrence in Africa can easily be explained in analogy to some bicontinental areas as due to the extinction of the representatives of the family in the region of the centre and their persistence in another continent. In this case they may originally have derived from the American part of the centre by the formation of an area of the type of the families *Mayacaceae, Rapateaceae, Velloziaceae,* etc., or from the Asian part of the centre by the formation of an area of the type of the *Aponogetonaceae, Dipterocarpaceae,* etc. Thus the existence of some areal exceptions cannot be said to disprove the conclusion at which we have arrived as to the centre of evolution of the origin of the Angiosperms. Today the following families do not reach this centre: *Achariaceae, Adoxaceae, Aextoxicaceae, Brunoniaceae Cercidiphyllaceae, Chlaenaceae, Corynocarpaceae, Crossosomataceae, Didieraceae, Empetraceae, Geissolomataceae, Globulariaceae, Gomortegaceae, Grubbiaceae, Heteropyxidaceae, Hoplestigmataceae, Hydrostachyaceae, Lactoridaceae, Limnanthaceae, Melianthaceae, Myrothamnaceae, Myzodendraceae, Oktoknemataceae, Oliniaceae, Pandaceae, Penaeaceae, Roridulaceae, Scytopetalaceae, Triplochitonaceae.*

The areas of the families thus contradict the picture of the surface of the Earth which Wegener has given in his theory of a continental drift, and it will therefore be necessary, however briefly, to deal with this theory. The question here is not whether Wegener's theory of a westward drift of the continents is correct or not, that is a matter for the geophysicists to decide and does not concern us, but whether the further arguments which Wegener uses for establishing his theory of the distribution and movements of the continents in the geological ages on his first theory are correct or not. According to Wegener the surface of the Earth formed prior to the Carboniferous one connected whole, which had one gigantic water desert, the Pacific Ocean. During the Jurassic to Tertiary Africa, Australia, Antarctica, India and Madagascar were separated from each other, while Africa and South America remained connected until the Cretaceous, when they became separated and began to drift apart. It will readily be seen that this theory is at variance with the distribution of the plant areas given above. The arguments which Wegener advances in support of this part of his theory are derived first and foremost from the distribution of the organisms, but he has for his arguments relied mostly on taxons lower than the family, and hence his arguments are irrelevant, as he deals with periods prior to the rise of the lower taxons. Moreover, in this connection it must also be pointed out that of the 120 families with disjunctive distribution 15 families, i. e. 12½ %, spread almost certainly across that part of the Pacific Ocean which according to Wegener's theory always has been a water desert! They are the families: *Eucryphiaceae, Goodeniaceae, Trochodendraceae, Lardizabalaceae, Epacridaceae, Stylidiaceae, Fagaceae, Balanophoraceae, Monimiaceac, Chloranthaceae, Elaeocarpaceae, Clethraceae,* and from among the Monocotyledons the *Centrolepidaceae, Restionaceae* and *Haemodoraceae.* To this comes the further fact that among these families there occur a number of types which are regarded as very primitive. This too would indicate the existence of a connection in this space and its subsequent interruption in the early euryplastic phase. Of course it might be argued that these families spread via Africa, but as we have no indication that they ever were in this continent, we must then assume that they later became extinct here, which raises difficulties of its own. Africa, according to Wegener's theory, was the cross-roads and centre where the greatest number of types accumulated, but he fails to explain how this can be reconciled with the fact that next to Australia it is also the continent which is avoided by the greatest number of families. It is true that the Pacific space interrupts the area of 69 families, and that thus it might be cited as an analogy in support of a one-time accumulation and later extinction of families in Africa; but the two spaces are not comparable, and the absence of the 69 families from the Pacific space can easily be accounted for by the present very small area of its islands and its uniform habitat, which is not favourable for the establishment of different plant types. Thus we must conclude that Wegener's theory of drifting continents cannot throw any light on the distribution of the areas of plants, and that the picture which he draws of the movement and distribution of the continents is at variance with the plant areas. This, however, is of less importance from the point of view of phytogeography, as these areas can be accounted for by the theory of land-bridges whose existence can be proved geologically.

We have thus arrived at the conclusion that the place of origin of the Angiosperms was probably situated in the South Pacific. Logically the next step in our enquiry should therefore be the time of origin of the families of the Angiosperms. Theoretically it should be quite possible to establish this. Unfortunately the Angiosperms cannot well be used for this purpose, as the earliest ones we know are already considerably advanced evolutionarily with a whole number of well-defined types, and as we have too few fossils for inferring their time of origin. Nevertheless we find in the Angiosperms indications of certain paleogeographical conditions, and by analysing the areas of their distribution it is possible to ascertain some continental connections. If the geological period of these connections could be ascertained, then it would be possible to determine the time of origin of all the Angiosperms. For such conclusions it would, however, be necessary to use also the material afforded by other old and paleobotanically better known groups such as e. g. the Gymnosperms. A similarity of the type of area of the Angiosperms and of the Gymnosperms would then indicate that they are of a similar age, and thus one could indirectly arrive at the age of the Angiosperms. One would, however, obtain still more exact and reliable results by using the very rich paleozoological material which we have, and which has been thoroughly worked and is adequately dated. From a comparison of similar area groups it is sometimes possible to infer also their simultaneous occurrence. Thus from the similar areas of plants and animals it is possible to infer similar geographical conditions, and thus also the geological age of the euryplastic phase of the Angiosperms in question. It goes without saying that only plants and animals which spread on land can come into consideration.

A further remarkable feature of the areas of the Angiosperms is their elongation in the direction along the parallels, which is due to ecological conditions. It is very rare to find in some families areas elongated in the direction of the meridians, but this too is closely connected with the ecological character of these families, as they represent often types bound to the coast, e. g. *Nolanaceae,* or to mountain zones of a north-south trend, e. g. the *Columelliaceae.*

These and other phenomena indicate the great stability of the ecological properties of some families. Often the ecological properties vary far less than the morphological character in such families. The persistence and variability of the ecological properties form two of the most interesting evolutionary phenomena. The basic ecological differentiation seems to have originated at the same time as the basic morphological features with the origin of the families, and sometimes still earlier. The ecological properties became, however, far more quickly stabilised than the morphological evolutionary vigour, so that today we find many morphologically different families which have rather similar ecological properties. As an example one may give here some families which grow so permanently in a certain environment that it is impossible to re-educate them for a different environment. Thus e. g. the whole group of the *Helobiae* is hydrophytic. Of the Monocotyledons the following families are predominantly restricted to the tropics and subtropics: *Palmae, Musaceae, Strelitziaceae, Zingiberaceae, Lowiaceae, Burmanniaceae, Philydraceae, Pandanaceae, Flagellariaceae, Taccaceae, Thurniaceae, Triuridaceae, Haemodoraceae, Restionaceae, Aponogetonaceae, Cannaceae, Marantaceae, Roxburghiaceae, Velloziaceae, Mayacaceae, Rapateaceae, Cyclanthaceae, Bromeliaceae, Alstroemeriaceae, Trichopodaceae, Stenomeridaceae, Hypoxidaceae, Apostasiaceae, Thismiaceae, Corsiaceae.* Predominantly tropical are also the *Commelinaceae, Hydrocharitaceae, Xyridaceae, Thecophilaeaceae, Pontederiaceae, Dioscoreaceae* and *Agavaceae.* Thus all in all 37 families from among the 67 monocotyledon families listed by Hutchinson are predominantly restricted to the tropics and subtropics.

Some families are restricted not only to the tropical zone, but are still more closely bound only to a certain ecological habitat. A number of families is characterised according to K. Suessenguth by the type of so-called "Drei Schrägstreifen-Areale" (after H. Wester). They are namely distributed in three strips, one in Indomalaya and Australia, the second in Africa, and the third in America, thus obliquely across the equator. They occupy the tropical regions of high rainfall of more than 1000 mm. in mostly non-mountainous territory, i. e. the regions of tropical rain forests. A number of families has adapted to these relatively circumscribed ecological conditions, e. g. the *Marantaceae* and *Cannaceae* from among the Monocotyledons, the *Anonaceae, Opiliaceae, Myristicaceae, Connaraceae* and *Lecythidaceae* from among the Dicotyledons. From an ecological point of view it is remarkable that these families quickly stabilised themselves ecologically, and that they developed only one ecological type, though they are often very ancient types which had the possibility of spreading where there was a suitable habitat, even though rather remote. The evolutionary capacity of the ecological properties declined here certainly far more quickly than that of the morphological properties, for they developed many genera but only one ecotype.

This great conservatism of the ecological character is a rather remarkable phenomenon in the evolution of the plants, especially when we remember that man has succeeded in many cases in transforming the ecological properties of many cultivated plants. This transformation is, however, more apparent than real, and consists mostly only in small modifications, which never enable the individuals with such a property to lead an independent life. Also in tropical plants "acclimatised" to the temperate zone it comes only rarely to the formation of strongly deviating ecotypes which would be capable of growing permanently outside the tropics. We find this sometimes among ruderal plants and agricultural weeds, e. g. in the genera *Galinsoga* and *Amaranthus*. But it is difficult to decide to what an extent we have here true acclimatisation and to what an extent a hidden ecological property which did not assert itself in the tropics. Some species of the genus *Solanum* may serve as an example; here we obtain sometimes from tropical species of lower latitudes varieties which are more resistant to cold than varieties obtained from mountain species. This is utilised for obtaining hardy sorts of potatoes by crossing with these types.

Theoretically we might expect all families to have the same evolutionary vigour, as they all formed at a time of high adaptability. Thus theoretically they should all have been able to spread around the whole world, as many families actually did. By evolutionary vigour, it must be remembered, we understand the capacity to adapt to the most different conditions and to form different ecotypes which are able to overcome obstacles in spreading. As, however, the evolutionary vigour was not the same in all families, and as its decline did not proceed at the same rate in all equivalent taxons, all families could not form quite the same areas. With a rapid decline of the ecological evolutionary possibilities in a family the representatives of this family did not change so quickly as to be able to penetrate as easily across different ecological zones as in ecologically uniform zones. Only about 75 out of the 303 families penetrated beyond the polar circle in the course of their development. The capacity to grow in a cool climate was formed presumably already in the euryplastic phase; but it seems that in most cases this capacity was formed in the present types not in the Arctic or Antarctic, but in the high mountains of the tropics. Later there was only a greater specialisation of this capacity in some types. This is indicated by the mostly bipolar character of these types, by the non-formation of families restricted only to the temperate or cold zones, as well as by the presence in the tropical and subtropical mountains of representatives of families reaching into the polar regions. The non-formation of families in the temperate and cold zones is a very strange phenomenon, and is probably connected with the fact that at the time of new-formation the regions around the poles were either sea or relatively warm. The non-formation of Arctic families confirms also the view of the gradual decline of the evolutionary vigour, for otherwise there would be no reason why new families should not have formed in cold regions, when genera were formed there abundantly, and species are still forming there today.

In the euryplastic phase, when the plants were considerably variable in all properties, the high mountains of the tropics and subtropics were constantly invaded by the species growing in their neighbourhood, which were able gradually to adapt to a cooler climate, and thus penetrated to higher and higher levels. In doing so they changed also their morphological features so much that new lines formed corresponding approximately to the families. When the climate grew cooler, and large cold and temperate zones formed at the poles, i. e. chiefly during the Tertiary, these mountain plants could easily get as far as into the temperate and even cold regions. The species which had already previously adapted to a cold habitat descended to lower levels and spread here often extremely quickly. Wherever such mountains bordered on the temperate zone, these mountain species spread latitudinally in the accessible plains. Their areas were mostly limited only by sea barriers. As in the Tertiary land connections between the continents existed especially in the north, they could easily spread over the whole temperate zone of the northern hemisphere. Sometimes as e. g. in the genera *Luzula, Carex* and others large regions of distribution were formed in the northern as well as in the southern temperate and cold zones, and these zones were linked together by some representatives of these genera growing in the high mountains of the tropics. It is only rarely in some families that one finds that localities in the tropics have not been preserved. The former connection is shown by their disjunctive bipolar area *(Empetraceae, Hippuridaceae, Sparganiaceae).* The tropics represent, however, mostly the primary habitat of these genera. Here they were, however, rare, though these high mountains of the tropics represent mostly the primary habitats of these genera. The mass occurrence of cool floras is very sudden, so that paleobotanically it may give the impression of the origin of new types of plants, especially as fossils of the ancient mountain floras are mostly lacking. After all, these were mostly herbacious types which could not easily fossilise. Thus only phytogeography and its study of the present areas of distribution can indicate how these types were formed.

In this connection it must be pointed out that different laws govern the distribution of the families and that of the genera. According to the conception of a decline in the evolutionary vigour one can assume in the genera at most the same, but mostly a much smaller evolutionary plasticity than in the family. Ancient genera which originated very early, already in the period of the formation of the families, by a rapid decline of the evolutionary vigour will probably indicate by their areas the same paleogeographical changes as are indicated by the areas of the families. On the whole this should, however, be rare, and has to be based on the assumption that evolutionary vigour did not proceed at the same rate in all corresponding taxons. As evolutionary vigour declined on the whole slowly, the areas of the genera should mostly reflect far later paleogeographical changes. That this is actually so is shown by a comparison of the areas of the families and genera of the individual plants with regard to the number of continents in which they occur. In the genera, conceived according to Hutchinson, the *Gramineae* and *Orchidaceae* were not included in the number, but it appears that their inclusion would not alter too much the general picture. For the families we reckon with 44 families according to H. Wester. In the Monocotyledons we then have the following numbers of genera and families occurring in one, two, three or five continents:

in one continent: 832 genera and 3 families
in two continents: 80 genera and 5 families
in three continents: 45 genera and 8 families
in four to five continents: 34 genera and 28 families

It is generally accepted that the areas of the taxons are the greater the older the types are. Of course this rule does not apply absolutely, but only in the great majority of cases. One can see at a glance that the above table bears out this rule, and that the numbers of genera and families are in inverse ratio to each other. Whereas the greatest number of genera occurs in one continent only, the greatest number of families are distributed in four to five continents. Thus this table shows too that the age of the families is far greater than the age of the genera, i e. that the families originated earlier than the genera. The above table is of course not exhaustive; if it were the differences in the distribution of families and genera would certainly be still greater, as intensively as families. We know also the great ecological plasticity types whereas in the cosmopolitan genera we have mostly young, ecologically strongly plastic types, which made it possible for them to extend their areas over the whole world. An exception is formed by the family of the *Convolvulaceae*, in which, according to Stebbins, ten out of the forty genera are pantropical. This on the whole rare exception indicates either a great age of the family or advantageous ecological properties of the genera.

If the genera and the families originated pari passu in the course of the ages, it could never come to such definite conditions as those shown in the table. Especially the striking increase in the families and the decrease in the genera are obviously the result of the different time of origin of these taxons. If there were here not a time distinction the numbers would rise regularly and not parabolically. In the Dicotyledons the conditions will certainly be the same. Without a time difference in their origin there is also no reason why genera should not have spread as intensively as families. We know also the great ecological plasticity of even the various cultivated species and weed species. Thus large areas are not a property only of the higher taxons. Exceptionally we observe this also in some families, e. g. in the family *Burmanniaceae*, which has a total of eight endemic genera distributed in America, and only two very aggressive species gave the family a distribution in the whole of the tropics.

When we take the number of genera in the different continents as the measure of the evolutionary vigour, and when we remember that the Monocotyledons without the families of the *Gramineae* and *Orchida-*

ceae have the following numbers of endemic genera in the various continents: America 359, Africa 190, Asia 184, Australia 91, Europe 8, then we see that it is just America which is by far the richest continent with a high evolutionary vigour, and this may be connected with the proximity of the centre of origin of the Angiosperms to America. In contradistinction to America the other continents are evolutionarily far quieter. Whereas Asia relatively loses, Africa gains; obviously a whole number of types arrived in Africa still with a high evolutionary vigour, and hence so many genera could originate here.

Finally we shall compare still the conditions in some of the species of a few families. Theoretically species too can arise by a sudden decline in evolutionary vigour already at a time when the formation of families predominated, and they can have maintained themselves, though of course rarely, until our time. In such cases these species would show similar areas as the families, and the areas of these species would reflect very ancient paleogeographical changes. Mostly, however, our present species originated in relatively recent time, and their areas will rarely indicate the land bridges which existed at the time when the formation of families or also of genera predominated. Most often their areas will be delimited by barriers which exist still today, i. e. chiefly by the present sea and mountains. Very probably the species originated throughout in more recent time. Thus in the tropical family *Taccaceae* we have two genera and thirty-two species which have small areas. *Schizocapsa* has one species in China; *Tacca* has twenty species in South America, three in tropical America, one in Hawaii, two in Africa, one in Madagascar, and finally there are three species with larger areas reaching from southern Asia into Australia. In this family most species have small areas; they differentiated in isolation from a relatively plastic foundation after the formation of the large area of the genus. Also the three species with larger areas have not particularly disjunctive areas. Obviously the formation of the species is here far younger than the types formed at the time of the greater evolutionary vigour of the genera, which had given rise to the disjunctive area of the genus.

A similar case is found in the tropical family *Pandanaceae*. Here we have 214 species in three genera. *Saraganga* is an isolated monotypical genus occurring in New Guinea and the adjoining Solomon Islands. *Freycinetia* has three species in southern Asia, two in New Zealand, two in Antarctica, and 60 on various Pacific islands. *Pandanus* has 63 species in Madagascar and the Seychelles, eight in southern Asia and Ceylon, 71 in Polynesia and Malaya, and four in Australia. Thus all the species, though they often grow on the coasts and can spread across the seas, easily form new species in isolated localities, and the origin of these species is probably of a young date.

We observe similar conditions in the larger family of the *Dioscoreaceae*. Here the genus *Dioscorea* has 293 species in South America, 163 in Asia, 83 in Africa, 32 in Mexico, and one in North America, 21 in Madagascar, 3 in Australia, and 2 in Europe. A larger distribution have *D. triphylla* distributed in Africa and Asia, and *D. bulbifera* distributed in the whole of the tropics. These two species were, however, spread probably only by cultivation. Of the other genera *Higginsbothamia* with one species occurs in South America, the monotypical genus *Bordera* in the Pyrenees, the genus *Epipetrum* with three species in Chile, the genus *Rajania* with twenty species in the West Indies, the genus *Tamus* with three species in the Mediterranean region. No species has a distribution which would indicate the paleogeographical land connections reflected in the genera and in the family. The species were thus formed at a far later time than the family and genera. Similarly J. L. Stebbins gives as a great rarity the occurrence of pantropical species among the 450 genera of the family *Orchidaceae,* among the 100 genera of the family *Araceae,* and among the 217 genera of the family *Asclepiadaceae.*

Conditions in the family of the *Juncaceae* are somewhat different. The small genera show a similar character of their distribution as in the preceding families. Thus the genus *Distichia* has three species in South America, *Patosia* one in South America, *Oxychloe* two in South America, *Prionium* one in South Africa, and *Rostkovia* one in the territory from New Zealand to Patagonia. The genus *Luzula* has twelve species in South America, ten in New Zealand, nine in Europe, six in Asia, four in North America, two on the Canary Islands, and one each in Hawaii, Tasmania, and the Azores. With a greater area we have two species distributed in the wider Mediterranean, seven species in the temperate zone of the northern hemisphere, and one collective species *(Luzula campestris)* distributed in Europe, Asia, North America, South America, Australia and Africa. In this genus we find already a far greater number of species distributed in large regions. This obviously indicates a greater geological age, as the circumpolar land connection shows itself clearly, and this ceased to exist perhaps already in the Miocene. The arctic connection seems here to be of a somewhat younger date than the antarctic connection. The connection between the two temperate and cold zones is via the tropical mountains of America. In view of the great age of this genus we cannot be surprised that it exhibits geographical modifications, though on the whole only small ones. Some authors regard all these modifications only as varieties of *L. campestris.* This species thus probably originated in the mountains of America and spread thence into the temperate and cold regions of both hemispheres already in remote geological times.

The genus *Juncus* shows still more markedly this type of distribution. Here, however, we have species of mostly humid habitats and predominantly of the temperate zones or of mountains. The hygrophile species spread mostly far more intensively than the species of dry habitats. Therefore we often find them distributed from the cold zones to the tropics, and among the hygrophile species we often encounter also cosmopolitan species. In the genus *Juncus* 61 species are restricted to North America, 38 to Asia (chiefly to the Himalayas), 27 to Africa (mostly to South Africa), 21 to South America, 15 to Australia, and 7 to Europe. From this it follows that the genus has its main evolutionary centre in the northern hemisphere in Asia and North America, with a secondary centre in the southern hemisphere, in South America, Africa and Australia. In the tropics this genus is rare and mostly restricted only to the mountains, but it is nevertheless just in these places that we must assume that the genus originated. The following numbers of species have larger areas: three species in Europe and Asia, ten species in the wider Mediterranean, twelve species throughout the northern hemisphere, two species in Asia and Australia, five species in North and South America, one species in South America and Australia, one species in Japan and North America *(Juncus xiphioides),* one species in Chile and in Formosa *(J. procerus),* one in North America, Asia and Australia *(J. falcatus),* one species throughout the northern hemisphere and South America *(J. balticus),* one species throughout the northern hemisphere, Australia, Madagascar *(J. effusus),* one species in North and South America, Australia, New Zealand and Europe *(J. tenuis),* one species throughout the northern hemisphere, South America, North and South Africa *(J. acutus),* one species throughout the northern hemisphere, North and South Africa, South America, Australia, New Zealand, Tasmania *(J. maritimus),* one species throughout the northern hemisphere, South America, Australia, New Zealand *(J. lamprocarpus),* and one cosmopolitan species distributed in the whole world, though only more rarely in the tropics *(J. buffonius).* Some species, and just those with the largest areas, spread mostly secondarily through the agency of man. They have namely tiny seeds whose testa becomes mucous when moist and easily sticks to the feet of animals, people and means of transport. The major part of their areas can thus be attributed to the direct or indirect action of man. Their great distribution is thus not due to the great age of the species. Especially *J. buffonius,* spreading however far more intensively by agriculture, *J. effusus, J. tenuis* and *J. lamprocarpus* spread in this way. On the other hand *J. maritimus, J. balticus* and *J. acutus* owe their large areas to their capacity to grow on salty soils of the sea coast, and thus they can easily enlarge their areas.

Even when we remember how easily this genus could spread, due to its having adhesive seeds, seeds so light that the wind can easily carry them, and access to suitable habitats, we have to admit that some extensive areas of species of this genus may have been formed already in remote times across land bridges. In the areas of some species a former connection of the northern temperate zone is fairly well discernible, in others a connection of the southern temperate zone. Thus it seems that some species are very old, and that the evolutionary vigour in this genus quickly died down. Favourable ecological properties suitable for expansion in on the whole all geological periods made it possible for some species formed in very remote time to persist till today. But even here we do not find species of which we can prove clearly that they are of the same age as the whole genus, and whose areas reflect all the former land connections across which the representatives of the genus spread. Most isolated localities are characterised at least by deviating varieties, considered by some authors to be new small species. Thus on the whole also this family does not contradict the assumption of a progressive decline in the evolutionary vigour from family to species.

Characteristic bipolar areas, restricted in the tropics mostly only to the mountains, occur also in the genera *Festuca, Poa* and *Carex*. In the genus *Carex* predominate according to Cain again species restricted to one phytogeographical region. It has 1281 species, and of these only 98 species have areas reaching into more than one phytogeographical region, though mostly only into adjoining ones. Of its remaining species 648 are endemic occurring only in one connected area each, i. e. more than half of all the species of the genus. The species of this genus do not appear either to have spread very early, for had they done so, it would have been shown by their areas. The occurrence of ancient species is thus already very restricted, and this agrees with the conception of the origin of the species later than that of the genus. Thus the species disappears far more easily than the genus, and the genus more easily than the family.

On the whole we may say that a rather large number of genera and also species soon lost their evolutionary plasticity, and that their areas are usually disjunctive. It is only fairly rarely that one encounters genera with a considerable plasticity, so that also in more recent time they could give rise to a fairly large number of species. In such cases we have, however, to deal with apomistic species or species with irregular heredity and not with species due to a meso-evolutionary increase of evolutionary vigour. Today we find also the species already considerably stabilised, and the formation of new good species is on the whole rare. Evidence of this stabilisation is that we have not any proofs of the origin of good species from the Ice Ages, which were accompanied by great climatic changes. Mostly we have here only small species formed by specialisation. Notwithstanding the great movements of the species at that time, we have no evidence of the rise of new species. Most of the species in the temperate and cold zones derive from a far older time, mostly from the second half of the Tertiary. In the literature we find many examples of the persistence of species from the Tertiary and, but only rarely, also from still older periods. The best known instance of such persistence from older periods is the discontinuity between East Asia and North America of some subtropical genera. These areas were according to Stebbins interrupted probably already in the Eocene, but prior to this we have the possibility of a connection of these two subtropical regions. Among very closely vicariating species Stebbins gives some with huge hiatuses. Thus *Erianthus maximus* from Polynesia has the closely related species *E. trinii* in South America. These types seem to have persisted already since the euryplastic phase. *Penisetum trachyphyllum* growing in Africa and closely related to *P. latifolium, P. bambusaeforme,* and *P. tristachyum* in tropical America seems to be a little younger. There exist very few such closely related species, and they can count only as exceptions. Their existence indicates the possible overlapping of the different phylogenetic stages in the evolution of the plants.

Phytogeography supplies important evidence for the existence of secondary centres of evolution, which can be accounted for by meso-evolution. Evolutionary aging does not proceed at the same rate in all taxons, nor in the same way. Some taxons lose their evolutionary plasticity very quickly, others very slowly, in others again there is a decrease followed by a temporary increase upon which a decrease supervenes again. We can trace evolutionary vigour only when it shows itself by the formation of many taxons, but these can be formed only under favourable outer conditions, as evolutionary vigour cannot assert itself without suitable conditions. If the conditions are not favourable, it either remains in abeyance or, if favourable conditions do not set in, it gradually dies away without having manifested itself. This we can tell from the distribution of the different taxons, which supplements well the knowledge of the evolutionary processes in the organisms. Very often the taxons are not uniformly distributed throughout the whole of their area, but are crowded together in some spaces, and represented in others by only a few members. Such a crowding together can best be explained by the appearance of a type which disintegrated into a whole number of related types, which then provided the foundation for the origin of new taxons, mostly equivalent to the original taxon. We can observe the manifestation of such an increase in the evolutionary vigour within all taxons, from the species to the highest taxons. The proofs for it are given in almost all taxonomic monographs. I shall give only one example, taken from the evolution of the genus *Sesleria*. This genus belongs to the affinity of the following genera, which are distributed in the tropics and subtropics, *Monanthochloe, Munroa, Echinaria, Orcuttia, Ammochloa, Urochlaena, Oreochloa, Fingerhuttia,* and *Elythrophorus*. The individual representatives of the genus *Sesleria* are ecologically on the transition between mountain and subtropical types; all of them grow, however, on rocks or slopes. The closest relatives of this genus, *Sesleriella, Psilathera* and *Oreochloa,* are already high-mountain to mountain species, and are distributed in Southern and Central Europe, especially in the Alps. Thus the genus *Sesleria* seems to have originated in the meso-evolutionary period of the family *Gramineae* in the mountains of the then warm regions, in which a small group of related genera arose in the high mountains of Europe, with the centre of evolution in the territory of the Alps, as all the related genera occur just here. The genus *Sesleria* had, however, the greatest evolutionary vigour, whereas the other, probably terminal members of this very uniform group of genera had already a weaker evolutionary vigour and produced at most a few, closely related species. The genus *Sesleria* formed, however, two sections. In the section *Argenteae* there are two groups of species. The first group, of six species, grows in the lower levels, and reaches as far as into the subtropics of North Africa. It thus shows ecological properties related to the original genera. The second group, also with six species, is restricted to mountain—high mountain sites. The whole section is distributed in the southern areas of the genus and has its centre in southern Europe. In the second section, *Calcariae,* there are all in all five groups of species. Three of these are eurythermic; they grow at lower altitudes, but ascend often to those of the high mountains. Their centre of evolution is in the Alps. The remaining two groups with eight species are explicitly high mountan groups: though they are connected with the Alpine centre, they have a prolific secondary centre of evolution in the Balkan peninsula. All the related genera and both sections of the genus occur in the Alps, but not with many species; it is here that the genus originated probably in the meso-evolutionary period of the family. Most of the species of the genus, but not the related genera, occur on the other hand in the Balkans. Thus the Balkan peninsula is the place of the secondary disintegration of the genus *Sesleria*. This example shows how the evolutionary vigour increased and then gradually decreased. The family of the *Gramineae*, which was formed in the macro-evolutionary period, disintegrated in the meso-evolutionary period into genera in various places, and the genera disintegrated in their turn in the micro-evolutionary period into species. The formation of the genera related to the genus *Sesleria* seems to be very old, and their present area is a relict area. Also the formation of the fundamental sections of the genus *Sesleria* is very old, and we can date the origin of some species according to the area at least into the Miocene. Thus the area of *Sesleria insularis* obviously formed in the Tyrrhenian continent, which broke up already in the Miocene, and though the individual localities were discontinuous no new species have developed since that time in the torn-off parts. For such a course of meso-evolution we find examples in almost all families and larger genera.

An analysis of the area of the individual taxons thus furnishes us with important information of a kind which no other branch of botany can give. An analysis of the areas of the higher taxons enables us to know at least something of the origin of the great evolutionary groups in the euryplastic phase, and elucidates the problems of micro-evolution and meso-evolution. An analysis of the lower taxons elucidates on the other hand those processes which are important for an understanding of the micro-evolutionary processes. Most of the baffling phenomena which we observe in the distribution of the plants are not at variance with the conception of an evolution in phases. On the contrary, many of them can be explained rather well by this conception, and phytogeography must thus be said to have contributed much to a clarification of the evolution of the plants.

The Basic Principles of the Evolution of the Angiosperms.

In order to be able to explain the development of the Angiosperms it is desirable to know the precursors of this group, as such knowledge would give us a firm foundation on which to erect the probable schema of the evolution of the group. However, no certainty has as yet been reached on this point. The *Benettitaceae, Cordaitaceae, Pteridospermae, Caytoniaceae, Gnetaceae,* etc. have all been suggested as possible ancestors of the Angiosperms. It seems, however, that in all of them we have a parallel development similar to that of the Angiosperms, but that they are not directly related to the Angiosperms. It is more probable that the Angiosperms had a separate evolution already from the simplest vascular plants, similarly as e. g. Florin describes it for the family Taxaceae. From the beginning they maintained themselves in a small number only. As we do not know the direct ancestors, we are restricted to the probable reconstruction by means of present types and also of fossil types. As in all other evolutionary lines we find that certain traces are preserved in the evolution of each group, and these have to be correctly recognised. This is, however, extremely difficult, and the danger of making incorrect generalisations is great. Nevertheless this is the only method by which we can at all hope to unravel at least to some extent the mystery of the ancestors of the Angiosperms. As all organs and properties are the result of evolution, it is possible by tracing their individual evolution to arrive at the primitive and derived features, and thus to gain an idea of the most primitive types of the Angiosperms.

The flower of the Angiosperm is most often regarded as of leaf origin, and its individual parts as transformed leaves. This view does not seem, however, to be correct. The origin of the flower of the Angiosperms has to be sought in the sporangia of the cryptogams, and cannot be derived from organs which developed from these. The sporangia must have changed directly into the flower. This evolution went via heterosporic types. From this point of view the euantic or pseudantic explanation is without any importance. The difference between the simple flower and the inflorescence is not greater than that between a simple and a ramified sporangium. One type can easily change into the other, and thus their division into two different categories does not contribute to an understanding of their evolutionary function. If they played a rôle in the evolution of the plants, it would be very difficult to explain the frequent change from flower into inflorescence and vice versa. The sporangium terminated the lateral or main axis and formed a specific organ of which the individual parts cannot very well be brought into relation with the axis or leaf. In fact, we might just as well try to explain the root as a transformed axis. In this way we should certainly not solve the whole problem. The modification of an axis is an axis, whereas a flower will always be the modification of a flower. Up till now we have no paleobotanical proofs of how and when the sporangia turned into the flower, but it is not excluded that such proofs may be discovered. The flower, so characteristic an organ in the Angiosperms, is, however, not restricted to this group, and we find similar organs also in some Gymnosperms; but probably this is a case of parallel evolution from a flower not resembling the original organs of the sporangium. The evolution of the flowers is one of the most controversial problems, and it seems that just in it lies the possibility of a correct explanation of the origin of the Angiosperms. So far, however, sufficient evidence has not been accumulated for its solution, and therefore this question remains open.

Also the origin and derivation of the leaves are explained very differently. There are three main views on the origin of the leaves:

(1) from flattened and concrescent twigs;

(2) from an appendage of trichomic derivation on the axis;

(3) from sterilised flower appendages, which in the course of evolution got into the vegetative axis, or from sterile appendages placed at the ramification of the axes.

The first mode of origin seems the most probable only for the evolutionary lines *Filicineae, Pteridospermae,* and *Cycadaceae,* where the sporophylls appear always in close relation to the leaves; the second mode of origin seems the most probable for some *Lycopodiaceae,* in which there is no relation between the leaf and the axial bud nor between the leaves and the sporophylls; the third mode of origin might perhaps apply to most of the other plants, in which there is always a direct relation between the leaf and the axial bud. In the Angiosperms the flowers are often explained as being macrophyll and related to the Cycas. It seems, however, that the agreement with the Cycas leaves is only apparent, and that we have here rather an evolutionary convergence, in which similar shapes arose in the terminal members. The anatomical agreement between the flower parts and the leaves, observed especially in types related to *Ranales* and interpreted so as to support a leaf derivation of these parts, should rather be interpreted in the opposite way, by the origin of the leaves from flower parts, or rather from the sporadium. In this case the leaves would only repeat a similar structure as they had originally in the flower, and it is also possible that the agreement of the vascular bundles in the leaves and in the flower parts need not indicate regression, but on the contrary progress. Evolution as it progressed was first directed towards a multiplication of the number of vascular bundles, and this carried necessarily with it also a new shape of the whole organ, e. g. in the leaves it led to a further strengthening and to a rich articulation of this organ. It seems, however, that the leaf of the Angiosperms arose rather by the expansion of flower parts and not of the whole axis in contradistinction to the macrophyll types. It is certainly more than doubtful if one can accept a double derivation of the leaves for the Angiosperms, all the more so as the uniform structure of their leaves indicates a monophyletic evolution. The problem of the origin of the leaves has, however, not contributed anything either to the elucidation of the evolution of the Angiosperms. The origin of the leaves is probably older than the origin of this group, and also many Gymnosperms are characterised by leaves which have had probably a similar evolution.

The formation of closed ovaries is a characteristic feature of angiospermy. But even this character is not unique in these plants, and arose obviously by parallel evolution in several evolutionary lines. Mostly, however, the angiospermous types did not maintain themselves long and soon became extinct notwithstanding their morphological and evolutionary complexity. It was only the Angiosperms, which spread strongly and pushed back all the other higher plants. Also in the Angiosperms angiospermy indicates a more advanced state. Sometimes, however, secondary gymnospermy could arise, as in the genera *Reseda, Butomopsis,* etc.

In the gynecium still another feature seems to be important, viz. the formation of apo- and syncarpic ovaries. It seems that just this feature may be very important for ascertaining the precursors of the Angiosperms. Already the first evolutionary progress of the Angiosperms is characterised by the great variability of this feature, and the first lines begin to establish themselves by its stabilisation. Thus this character seems to be as important as the development of the tracheae and tracheidae, the number of placentas, etc. Apocarpy or symptoms pointing to it by the imperfect concrescence of the ovaries, and by stigmata or at least arms in the number of the carpels seem to appear in a number of plants characterised also by a great variability of some other basic morphological characters. Therefore it seems that apocarpy arose in the first period of new-formation, and that it may point also to the precursors of the Angiosperms. Thus this character is very important taxonomically, and its valution is one of the most important means for evaluating the taxons. The value of the morphological characters for judging of relationship varies, however, very much. The only fairly reliable means for valuating morphological characters, and really all characters and properties, is to ascertain their function in the plants and then to judge of their relationship. For this it is necessary to select groups in which the greatest possible number of qualitative and quantitative characters occur. Here almost agreeing individuals will most often form a species, individuals agreeing in the qualitative characters a genus ,and types agreeing only in certain qualitative characters a family, etc. Unfortunately it is not possible to make a perfect classification by this simple statistical method alone, for we are not dealing here with the classification of an anorganic mixture but with the classification of living organisms. The behaviour and mode of life of living organisms are very complicated, and in the evolution of the organisms we observe so many modifications and exceptions that the taxonomist must combine the exactness of a scientist with the sensitivity of an artist. A conformable evolution in different lines, the appearance of qualitatively the same basic features in taxons of all categories, the impossibility of experimental verification of the higher taxons will always cause great uncertainty.

One of the most characteristic features of primitive families is the great basic variability of all essential characters. The characters became stabilised at different times and in different members in the course of evolution. Families whose individual representatives have a great number of basic modificatins are evolutionarily older than families which are on the whole uniform; this is a consequence of the stabilisation of the evolutionary vigour. We have to assume that in the beginning all features capable of change were unstabilised and variable. Soon, however, some features began to stabilise themselves hereditarily, not succumbing to further changes. Thus when a group forms taxons of closely related types and exhibits many modifications of those basic organs and morphological characters which are very constant in other taxons, we know that it originated at a time when the characters were unstabilised, and that it is thus from an evolutionary point of view older than a group which has a more uniform structure of the organs. Such characters are e. g. apo- and syncarpic ovaries, flowers built according to different numbers, numbers of circles and of their members, diversity in the basic structure of the axes, leaves, different in the number of placentas, different types of inflorescence, differences types of pollen grains, great number of related taxons, etc. This phenomenon may be a very great help in judging whether a family is primitive or derived. From this point of view we often come also to a different valuation of some higher taxons than one now current. On the basis of this we can divide all taxons into two groups, stenomorphic and eurymorphic ones. The former are morphologically uniform and mostly also more derivative, while the latter will exhibit more qualitative and probably more primitive morphological characters than the former.

An interesting evolutionary question in the Angiosperms is whether the woody types or the herbaceous types are the more primary. The families including wood plants retain sometimes more primitive characters than the herbaceous families. It seems as if the formation of woody axes had caused a rapid decline in evolutionary vigour, and hence the stabilisation of some characters. In connection with the woody character also certain flower types usually become stabilised; sometimes these characters are obviously primitive as in the Ranalian taxa and *Amentifereae*, or relatively more stabilised as in the Monocotyledons. Here the families of the woody types *(Palmae, Dioscoreaceae, Agavaceae, Ruscaceae, Philesiaceae, Velloziaceae)* form mostly flowers with a structure which approaches the one most characteristic for the flower of the Monocotyledons. Such flowers have a stabilised number of circles and members. Also the woody types of predominantly herbaceous families have flowers which approach most the structure of the flowers of the Monocotyledons, thus *Puya* from among the *Bromeliaceae*, *Pothos* from among the *Araceae*, *Prionium* from among the *Juncaceae*, *Bambusa* from among the *Gramineae*, etc. Thus it seems that there is a correlation between a ligneous character and the structure of the flower, and that this particular structure of the flower represents a predisposition and evolutionary trend in the woody types. It seems, however, that in different evolutionary lines the relation between flower structure and lignification was different. It is probable that the lignification of the axes became fixed in different evolutionary lines differently, and that this character can be evolutionarily conserved in different evolutionary phases, and thus can have also different taxonomic significance. It is difficult to arrive at any firm conclusion as to whether the woody types are more primary than the herbs or not; nevertheless it seems more probable that the herbaceous types were earlier, and that only by the formation of woody types the discovery of the Angiosperms by paleobotany became possible; but at once when the progress of Angiosperms occurred woody types were formed. Thus in these also characters could maintain themselves which are regarded as more original. As, however, every character can appear in a different evolutionary value, so also this character certainly often arose only later, and then it is characteristic for lower taxons.

The relation between the morphological structure and an aquatic environment is also very close. In expressly aquatic families characters regarded as primitive have been preserved relatively abundantly in the Dicotyledons as well as and especially in the Monocotyledons. Here probably the uniform environment precluded the origin of many orthogenetic lines, and only the basic evolutionary principles could assert themselves, while their habit too is restricted to only a few types. The uniform environment caused probably also a simplification in the evolutionary potency as it shows itself, and directed it into a smaller number of types, as a great divergent evolution which causes specialisation is impossible in a uniform environment, which thus considerably limits the evolutionary possibilites. For the taxonomy of the plants this is, however, advantageous, as these types permit a better reconstruction of the basic evolutionary processes. As an example may be given the group *Helobiae,* where the aquatic environment acted as a stabilising factor. It was not favourable for the formation of multiform vegetative organs. The sex organs changed, however, and mostly formed the basic types which we observe also in other Monocotyledons, but there was no such great disintegration into many morphologically different quantitative modifications as we find in the terrestrial types. Thus all basic qualitative types arose in the aquatic environment, but this did not provide the opportunity for the evolutionary vigour to unfold richly. Thus the environment caused here changes in the quantitative representation, but did not call forth any qualitative changes. Wherever we have an evolution of this type it is of great assistance to taxonomy.

The problem of the relation between the Monocotyledons and the Dicotyledons has not been definitely solved. It is generally accepted that the Monocotyledons separated out from the older Dicotyledons at a very young evolutionary stage, but from the point of view of evolutionary development this does not provide any satisfactory solution of the problem of the relationship between the Monocotyledons and the Dicotyledons. It seems that at the very beginning of the evolutionary progress of the Angiosperms several evolutionary lines differentiated, one of them being the Monocotyledons. Semewhat extreme characters developed in these, and thus they rather diverged from the other groups of Dicotyledons. The Dicotyledons seem to be not a uniform evolutionary group, but were differentiated probably into three groups, evolutionary equivalent to the Monocotyledons. The origin of all groups was probably contemporaneous.

It appears that evolution did not proceed simultaneously in all organs of the plants. The evolution of the sex organs, leaves and root shows sometimes a different stage of advance in their structure. Thus it seems that the individual organs developed independently enough. If we assume that the flower parts originated from modified leaves, then both organs, the flower parts and the leaves, should show at least some dependence on each other, but this is not the case.

It seems that it is an overestimation of the importance of the structure of the flower and the changes it underwent to rely solely on these as criteria for establishing relationships. It is true that in many types there is really a correlation between the structure of the flower and the affinity, which might be used as criterion, but in others the correlation is entirely insufficient as a criterion. As example may be given the families *Liliaceae* and *Amaryllidaceae,* which are distinguished according to the structure of the flowers; the type of their inflorescence proved, however, a far better distinguishing character than the structure of the flowers.

The taxonomy of the Angiosperms is so very difficult a problem because they are a relatively young group in which the basic organs are very variously metamorphosed, and because they have many parallel evolutionary lines; hence a simple general survey of the evolution of this group is made particularly difficult. On the other hand the study of the evolution of this group can elucidate the evolution of earlier groups whose evolution was governed by similar laws, but of which many representatives became extinct in the course of time.

Present taxonomy aims at arranging the plants in a system which will show their generic place, the lines starting from the respective ancestors, the value of the taxons according to the agreement and disagreement of the various organs, and thus to establish a natural system of the plants. This is by no means easy, largely because the present plants are only the remnants of those which formerly existed and represent their terminal links. Thus the better we know the history of the plants, the more accurate will be the system we build on them.

The most important means for discovering the relationship between the plants are the morphological characters, as it is assumed that related plants have similar basic morphological characters. Formerly the greatest emphasis was therefore laid on comparative morphology. But this approach has the disadvantage that convergent types may be placed as related types. Today we know that similar characters can be formed in quite unrelated lines whose evolution proceeded similarly, probably under the influence of the material predisposition of the living matter. A considerable difficulty in building up the system of plants is the disagreement between morphological structure and relationship. The assumption that the more complicated the morphological structure, the more derivative must be the type need not be correct. Though in many cases a simple type appears at first which only later becomes complicated by orthogeny, increasing simplification may also occur or most often there comes a sudden disintegration into complicated and simple types. Most often the origin of new types appears suddenly, just as in a genetic or morphological experiment a type may suddenly disintegrate into a number of new ones. When this is the case, a whole scale of basic modifications forms suddenly and not gradually in successive generations. Gradually some of the modifications perpetuate themselves, while others disappear, but mostly no new qualitative modifications appear.

The origin of polyploids may serve as an example. Mostly there do not arise here successive polyploid lines of di- tri- tetra- penta- to polypoids, but mostly immediately in the first generation an octoploid originate from a diploid form or also a whole series of different polyploids. In the course of time, however, some types become extinct while other types persist. Thus disintegration sets in suddenly, and, mostly already from the beginning of the evolution of a plant, basic qualitative modifications appear of which some become fixed in the course of evolution. The situation is probably similar in phylogeny; at the very beginning of evolution a number of modifications originate, of which some become gradually stabilised in the following generations. In the course of this process some characters, just as some pure lines, may become separated out. Characters which we find today firmly fixed in the individual taxons are already firmly stabilised, and exhibit the evolutionary possibilities of the primary types. Thus taxons in which we find a greater number of different characters were formed at an earlier time from the point of view of evolutionary vigour than taxons whose characters are simple. Therefore the fixed characters constitute an important guide to the evolutionary processes. It is possible to assume that the taxons with many different characters derive from a time with a greater evolutionary vigour of their ancestors than morphologically uniform taxons.

The lack of connecting links in the higher taxons renders investigation here particularly difficult, as it debars us from ascertaining the relationships accurately. But in the lower taxons transitions are frequent, and thus affinity groups can on the whole be well defined in them. The lack of gradual transitions in macro-evolution is a general feature and may be caused by the sudden disintegration into dissimilar types, whose differences become still greater in further evolution. It appears that in macro-evolution evolutionary leaps were frequent, whereas in micro-evolution a gradual development was more frequent. The evolutionary leaps cause always considerable difficulties in the taxonomic valuation of the higher groups, and therefore we are faced with so many different valuations in some taxons.

At the height of new-formation in the Angiosperms, a number of representatives of different evolutionary lines arose almost simultaneously, and these should be valuated also taxonomically as equal. Very probably several lines were formed here from the original stock, and not only two lines corresponding to the traditional division of the Angiosperms into Monocotyledons and Dicotyledons. The Monocotyledons represent an evolutionarily rather uniform group, characterised by some rather extreme characters as compared with the other groups. It appears that the Monocotyledons separated out from the rest of the stock just as the family *Orchidaceae* separated out from the *Liliaceae*. But the rest of the Angiosperms does not form one single group corresponding to them, but rather several parallel groups of the same taxonomic valence as the Monocotyledons. As, however, in none of these groups there were strikingly distinguishing features, they are most often regarded as one group, just as the taxons of other evolutionary lines are often placed in the *Liliaceae*, though their non-homogeneity becomes clear in a detailed analysis of all of the characters. It appears that at the beginning of the evolution of the Angiosperms not only the Monocotyledons separated out but also the Ranalian taxa, the Centrospermian taxa, and the *Amentiferae*, and probably also others, all of which are taxonomically equivalent. In each of them we find also a rich division of the higher taxons, indicating their high taxonomic value. The question as to the primacy of any one of these evolutionary lines is irrelevant, for probably they originated simultaneously and are characterised by a similar evolutionary vigour and thus also by a great number of basic types. The rich division of the lower taxons is, however, rather the result of the action of specialisation, and thus of the overmultiplication of suitable types and suitable orthogenetic lines.

In judging of the relations of the basic evolutionary types we mostly do not find a continuous series of transitional characters and thus clear relationships, as we often find it in the lines of the lower taxons. This phenomenon too can be explained by evolution. In the euryplastic phase even rather considerable modifications may be phylogenetically closer to each other than modifications which are rather alike in the period of the stabilisation of the evolutionary vigour. With the decreasing evolutionary vigour also the magnitude of the modifications will gradually decrease, and the relationship will thus become clearer. In the euryplastic phase, on the contrary, also considerable modifications will be often phylogenetically closer to each other than modifications in the micro-evolutionary phase, when convergent evolution may cause an apparent affinity. Thus the magnitude of the morphological modifications need not be in many cases in direct proportion to the relationship, and two great morphological modifications may be genetically closer to each other than small modifications due to parallel evolution in distantly related lines.

The higher units are built on common characters which are more or less constant, and of which it is assumed that they characterise genetically homogeneous lines. The danger of compiling heterogeneous lines on the basis of an incorrect or artificial valuation of the characters is considerable. Thus e. g. the *Aristolochiaceae* and the *Dioscoreaceae* have some characters in common, and it is here possible to assume that we have either convergent similarity or direct affinity. This is very important for taxonomy, as in the first case we get a monophylletic development of the Monocotyledons and in the second case a biphylletic one.

Each organ and also its part can pass from evolutionary plasticity to evolutionary stability, and then it indicates certain groups which started from them. It seems that in the plants simple and complex forms originate equally easily, and both are often contemporaneous. Complex forms seem, however, to have had a longer orthogenetic evolution, and often their evolutionary vigour is of long duration. Therefore it takes a long time before the evolutionary possibilities of such complex forms become organised so purposively that the plants can have a mass increase, and hence these plants persist for a long time only in small numbers. The result of this is that the origin of complicated taxons is discovered paleobotanically mostly only far later than the evolution of simple ones which can assert themselves quickly.

Another interesting property which we observe in the evolution of the plants is the conservation of the changes in different evolutionary phases and their different genetic and taxonomic significance. One and the same character can be, as already said above, in different taxons a character of the highest to the lowest taxons. The higher the taxon the less variable are such characters. The characters of the higher taxons are therefore mostly not accessible to genetic experiments, whereas the characters of the lower taxons are subject to genetic laws. This is a very striking difference. It looks as if the characters fixed themselves in quite different ways, and as if the characters fall into two groups, inner ones which are not subject to variability, and outer ones which are variable and subject to genetic laws. It seems that the basic structure of the whole skeleton of the organism rests on the first group of characters, and their changes cause mostly the organism to perish. The difference between the inner and outer characters may be due to basic differences, as we find them in anorganic wholes, e. g. in atoms and compounds. Here we have likewise an almost unchangeable nucleus and an envelope changeable by outer conditions. In the plants the properties situated inside do not change, are constant, and thus have a great taxonomic significance. The outer ones on the contrary are subject to variability, become taxonomically more subordinate, and characterise the lower taxons. So far it is, however, quite obscure which character or property passes into the inner and which into the outer structure of the living matter, and in what way this takes place. It seems that in the course of the aging of the taxons the inner properties constantly increase in number. On this principle will probably rest also the possibility of liberating or rather renewing the evolutionary vigour, i. e. the possibility of the origin of higher taxons. All that is known today about the metamorphosis of the species concerns the group of the outer properties and refers mostly to a recombination or loss of changeable outer properties and shapes. These give mostly rise only to the origin of taxons lower than the parent species. These outer properties belong mostly to specialisation and not to evolutionary progress. An interference with the inner evolutionary dynamics must, however, have a many times greater influence on the change of properties and evolutionary possibilities. We do not, however, govern this liberation of evolutionary vigour, and it seems that so far all interference with the inner properties leads to death. It is, however, not excluded that once it will be possible to interfere so effectively with living matter that one can increase its evolutionary vigour, at any rate to a limited extent.

The Evolution of the Monocotyledons.

Especially of late the Monocotyledons have been regarded as an inhomogeneous taxon which has originated from two or three different evolutionary groups of the Dicotyledons. Thus Kuprijanova on the basis of pollen analysis ascertained even four evolutionary lines, three starting from Dicotyledons *(Piperales, Polycarpicae, Ranunculaceae)* and one from the hypothetical group of the *Proangiospermae*. In addition to these taxons some authors accept also a possible origin of the family *Dioscoreaceae* from the family *Aristolochiaceae* or *Menispermaceae*. A monophylletic evolution with an origin from one ancestor seems, however, far more probable than such a polyphylletic evolution. Almost all families of the Monocotyledons show a very uniform structure, and it is difficult to assume that this structure originated from different evolutionary groups. Nor is any case known of a monocotyle plant having been successfully crossed with or grafted into a dicotyle one. On the other hand it is quite possible to place all Monocotyledons in mutually related natural evolutionary groups. The evolution of the Dicotyledons proceeded along different paths than that of the Monocotyledons, though some basic groups are strikingly similar to each other. This is, however, natural, as the Dicotyledons and the Monocotyledons have a common origin, and thus also some types may be fairly closely related. Just the *Ranales* and the *Helobiae* show a similar evolutionary trend. Some *Polycarpicae* and *Cabombaceae* have trimerous flowers and apocarpic, spirally arranged ovaries. From this mere relation we cannot, however, deduce the relative age of the two groups. With equal justification one might assume that the Dicotyledons were older than the Monocotyledons or younger. Something may be said for and against each of these groups being the older or younger one. Most probably the Monocotyledons separated out at the same time from the common stock as the Dicotyledons. Then both groups developed further independently of each other. An interesting difference is given by the characters which we regard as primitive having been preserved in the Dicotyledons mostly in the woody types, whereas in the Monocotyledons in the herbaceous ones. These characters are not only the apocarpic ovaries and their cyclical arrangement, but also the anatomical structure. In the Monocotyledons tracheae lack in *Elodea, Vallisneria, Lemma perpusilla, Spirodella, Najas, Ruppia, Zannichellia,* and *Zostera.* Though these are aquatic plants, yet the trend to the loss of the tracheae is certainly remarkable, especially as they are well developed in many other aquatic plants. Also a primitive structure of the flowers without any regular alternation of the circles or naked flowers are frequent in the families which we regard as more primitive *(Potamogetonaceae, Araceae, Najadaceae,* etc.).

The investigation of relationship and taxonomic position is the first condition for a correct understanding of each taxon in nature. When ascertaining the relationships we have mostly to rely on the present properties of the plants, which manifest themselves in the different morphological structure, ecological properties, distribution, etc. In the lower taxons with their numerous, very close relations this is comparatively easy. But in the higher taxons we meet with difficulties, as the relationships may be obscured by convergent conformable development in different evolutionary groups, which are sometimes only very distantly related. The evolution of each great taxon may also have proceeeded in such different ways that the mutual relations are not clearly visible from the present types. This also interferes with a simple general survey of the evolution of the great taxons. The differences between the higher taxons are mostly not unequivocal. In each such taxon we find at least indications of evolutionary trends which are found also in other evolutionary groups. This is due to the material predisposition of each evolutionary group and to the relatively small number of the possible qualitative modifications. Thus the definition of the groups of relationship is rendered doubly difficult, and controversy will always arise as to how best to solve individual cases. We do not know the precursors of the Angiosperms for certain, and thus there is not either a generally accepted view as to the morphological character of the first flower. Also the definition of the basic types and of their successive changes is more or less guess-work. Notwithstanding these difficulties the system erected is in principle correct, and it is really now only a matter of making it more and more accurate.

The rise of long evolutionary lines seems to be improbable. Disintegration took place suddenly, and the basic evolutionary groups differentiated suddenly at different levels of the plastic stock. These groups are thus connected by relationship only through this plastic stock. Evolutionary lines compiled on the basis of morphological resemblance are mostly only apparent, not real. Mostly we have here a parallel evolution of lines which had differentiated independently already at the stage of the plastic stock. The origin of an unstabilised group from a stabilised one is little probable. Therefore the taxons which are taken to be the initial ones are those which show unstabilised conditions. The stabilised ones are regarded as the predisposed type to which the evolution of the Monocotyledons is directed. From this point of view types with clearly reduced structure of the flower, such as the *Orchidaceae* and the *Scitamineae,* are regarded as imperfectly differentiated predisposed types. Notwithstanding the immense complexity of their flowers they cannot be regarded as representing the evolutionary goal. They are only types in which a not normal, irregular evolution stabilised itself, leading often to a great instability of the whole structure of the flower. Thus they are evolutionary groups which deviated in evolution into a lateral possible road. They may have a considerable vitality and play a prominent part in nature. But they do not represent the evolutionary termination which is directed towards perfect regularity due also to material structure. All in all three types can be regarded as the basic groups from which evolution started. First and foremost we have here the group composed of unstabilised types of an on the whole simple structure with the *Helobiae* as prototype. The second group consists of the stabilised, pentacyclic, trimerous types with regular flowers and syncarpic ovaries with the *Liliaceae* as prototype. The third group comprises the irregularly developed types with the *Orchidaceae* and *Scitamineae* as prototype. But up till now nobody has tried to start from this third type. According to present views such a development is not even probable. Thus there remain only two starting groups. The primitivity of the *Helobiae* is generally accepted. But for the other, similarly built families *(Araceae, Palmae, Eriocaulaceae,* etc.) it is often admitted that they originated by reduction from pentacyclic, trimerous types. Thus we get frequently a heterogeneousness in the whole taxonomic structure. On the basis of the Ranalian theory one admits that the *Helobiae* are the most primitive, but that they led to the other groups, mainly via the *Liliaceae.* The types of an irregular, complex, build such as the *Orchidaceae*, *Scitamineae*, etc. are regarded as the evolutionarily most advanced ones. This system of the plants is governed chiefly by the conception of the complexity of the structure of the flower. This does not seem, however, to be directly proportionate to relationship. In the primitive types, e. g. in the *Hydrocharitaceae*, we often find types of equally complex structure as in the *Orchidaceae*. Complexity in the structure of the flower is rather an evolutionary exception than the rule and may arise in all evolutionary phases. Mostly it does not indicate relationship, but only an analogous modification of the normal evolution.

The most frequent systems are those in which the family *Liliaceae* occupies a central position, and these systems have a firm structure. The apocarpic types are on the contrary not used as an initial evolutionary group on which to erect a system up to the evolutionarily advanced types. Mostly they pass soon into the *Liliaceae*, and only then do they diverge. Simple flowers, except the *Helobiae*, are mostly explained by reduction or by atavism. The drawback of a system in which the *Liliaceae* occupy a central position is that it easily leads to an overestimation of similarly built perfect flowers, which results in convergent and not directly related types being included in the family *Liliaceae* or in its affinity as in close relationship. In these cases it has not been fully taken into account that the evolution of all Monocotyledons is directed towards one definite, stablest type in all independent evolutionary groups.

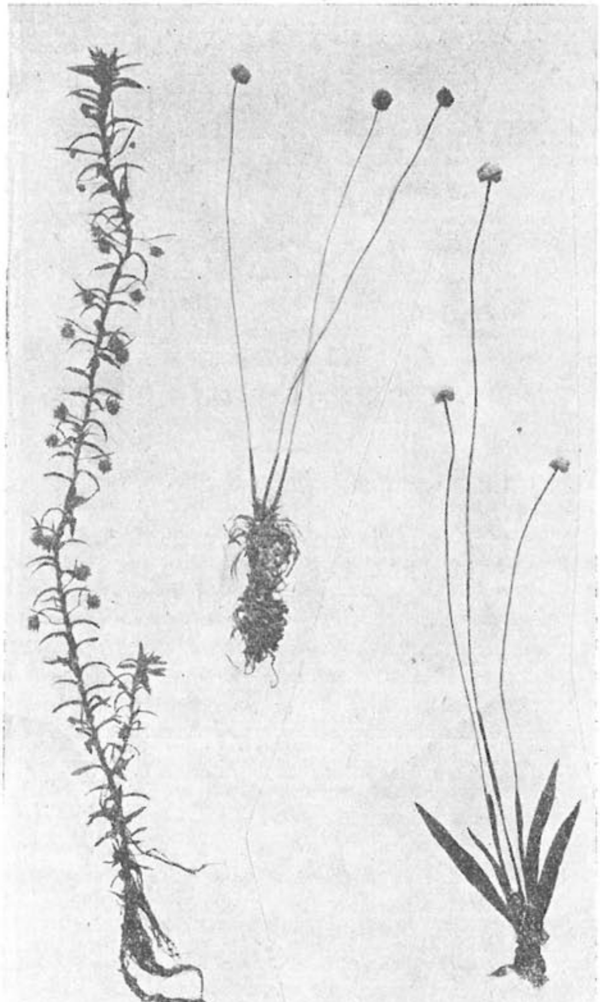
This leads us to consider the problem raised by convergence, which is the most baffling problem of all in taxonomy. Many cases will certainly for long defy solution. Some types will remain heterogeneous for long, and their placing has to be decided simply according to similarity of structure. But they may be types in which similar morphological forms appeared by predisposition, though they derive from different ancestors. The possibility of such a parallel development can be assumed in all types which do not fit into the dispersion of the variability observed in the other species of the taxons. Here it is of course not the magnitude of the modifications which is of importance, but rather the evolutionary trend of these modifications.

Certain shapes of the predisposition to their formation are most often passed on uninterruptedly from generation to generation. Sometimes, however, such shapes occur independently of affinity, and are due only to the similar material composition and to the evolution based on it. In nature, however, there are not individuals forming a continuous transition, but the individuals form definite wholes, which again form a coherent system from the species to the families and the higher taxons. The lower the taxon, the greater is the material, morphological and physiological agreement of the individuals. The characters or dispositions transmitted by the ancestors are transmitted continuously from taxons to taxons, but decrease gradually in number. It is on these characters that the system of the plants is built first and foremost. Such relations also do not cause any taxonomic difficulties. It is far more difficult to solve the problem raised by the characters which appear intermittently in the descendants. These are based mainly on predispositional evolutionary changes due to the uniform material composition. Thus they may occur in the same configuration also in groups not directly related. It is just these characters which condition the convergent evolution of different lines, and thus constitute the most difficult problem of taxonomy. Their occurrence is of course also governed by law, and hence these phenomena too can be used for taxonomy.

The closer the affinity of the taxons the more similar is mostly the appearance of such characters. This rule is, however, already less invariable, and sometimes strange convergences may occur resulting in obviously distant groups agreeing in many characters. Such cases have always to be investigated most carefully if fundamental mistakes are to be avoided. Such strange convergences we find e. g. in the families *Aristolochiaceae* and *Menispermaceae* on the one hand and in the family *Dioscoreaceae* on the other hand. Often even two related families do not have so many characters in common. Thus the shapes of the leaves, the lianic character, the trimerous flowers, the inferior ovary, the similarly formed capsule, the frequent monocotyledony and dicotyledony, the serial buds, and the secondary thickening are all similar in the two groups mentioned above. Nevertheless when it comes to determining the relationship of the families of the two groups we arrive at the conclusion that we have here only a remarkable convergence. This is probably caused by the lianous habit of both groups. But there are on the whole few such strange convergences. Usually only isolated characters are similarly organised in distant evolutionary groups. There is here little probability of a conformable evolution in two non-related groups, as evolution is always conditioned by a great number of different causes and their consequences. Of course the closer the affinity the more often we have a similar variability of the characters. Vavilov called this phenomenon homologous variability. Here the greater the affinity the more homologous the variability. This may even enable us to expect that some characters will occur in closely related types. Sometimes homologous variability may manifest itself very markedly also in families. When so, it enables us to determine the affinity of the families which show the same homologous variability. As far as affinity is concerned, the evidential value of homologous variability is particularly clearly seen when it extends to unusual characters. In the Monocotyledons an example of such a homologous variability, and of its value for establishing affinity, is given by the families *Eriocaulaceae* and *Xanthorrhoeaceae.*

The aspect of the individual representatives of both families is strangely alike. This likeness is really remarkable, as the two families have an entirely different ecology. The *Eriocaulaceae* are swamp and aquatic types, whereas the *Xanthorrhoeaceae* are explicitly xerophile types. We shall consider here the three basic physiognomic types:

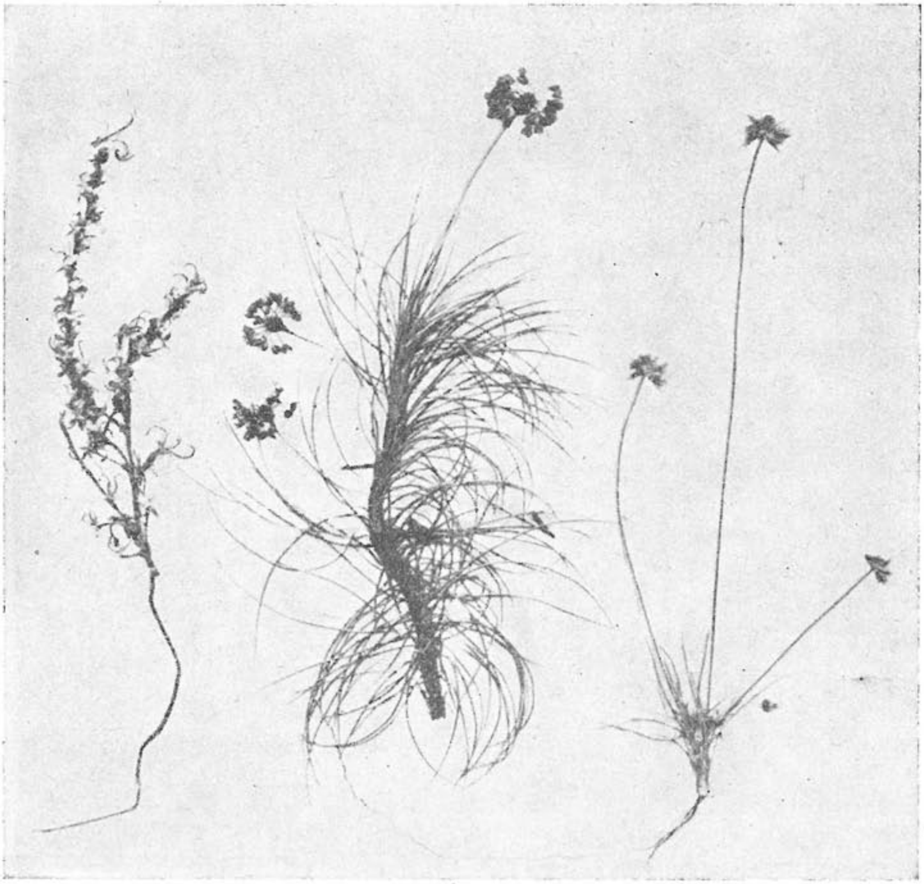
(1) leaves long, in the basal rose and from it grow long stalks with dense terminal heads of flowers which have at the base covering bracts. Among the *Eriocaulaceae* this type is especially represented by various



Phot. 1. — Homologous variability of the families *Eriocaulaceae* and *Xanthorrhoeaceae.* Convergent types of the family *Eriocaulaceae.* From right to left: *Tonina fluviatilis* L., *Eriocaulon Wightianum* Meet., *Paepalanthus Turckheimii* Ruhl.

species of the genus *Eriocaulon.* Among the *Xanthorrhoeaceae* various species of the genera *Xerotes* and *Chamaexeros,* and some species of the genus *Lomandra* have a similar aspect. *Aphyllantes* is a similar type, but with larger flowers.

(2) The stem leaves are dense and mostly shorter. From them grow long axial stalks terminated by flower heads. Among the *Eriocaulaceae*



Phot. 2. — Homologous variability of the families *Eriocaulaceae* and *Xanthorrhoeaceae*. Convergent types of the family *Xanthorrhoeaceae*. From right to left: *Laxmannia sessiliflora* Denk., *Alania Endlicheri* Kuth., *Laxmannia squarrosa* Lindl.

this type is especially represented by various species of the genus *Paepalanthus,* among the *Xanthorrhoeaceae* by *Borya, Sowerbaea,* and some species of the genus *Laxmannia.*

(3) Stalk leaves short, and between them grow very short bracteal stalks, not longer than the leaves, terminated by flower heads. Among the *Eriocaulaceae Tonina fluviatilis* is a typical example, among the *Xanthorrhoeaceae* some species of the genera *Acanthocarpus* and *Laxmannia.* Also *Calectasia* is of a similar type, only the flowers are larger.

But the aspect is not the only common character, also the structure of the flower shows a homologous variability. In both types the flowers have a dry, often hairy perianth not differentiated into a typical calix and corolla. The individual circles of the perianth are, however, considerably differently organised. Also the shape of the pollen grains is in both families very similar.

Aphyllantes has pollen of spiraperturate, baccate shape, spined. This is a rather unusual shape occurring with a similar organisation also in *Lomandra.* The latter has the pollen zonisulculate to somewhat spiraperturate with irregular minute spines. The remaining genera of the *Xanthorrhoeaceae* have monosulcate pollen *(Borya, Dasypogon, Calectasia,* etc.) and bisulcate pollen *(Acanthocarpus),* sometimes also zonisulcate pollen *(Chamaexeros, Lomandra, Kingia).* In the *Eriocaulaceae* the pollen is mostly spherical, spiraperturate, with minute spines as in *Aphylanthes* and *Lomandra.* Or again pollen of similar shapes as in the *Xanthorrhoeaceae* occurs also in the related family *Xyridaceae.* The genus *Abolboda* has an uniporate, spherical, spiny pollen somewhat reminiscent of the spiny pollens of the preceding families. The genus *Xyris* has uni- to bisulcate pollen, not spiny, somewhat similar to that of some genera of the family *Xanthorrhoeaceae.* Thus palynology makes it possible to obtain in this case absolute confirmation of the agreement which is indicated also by the morphological shapes.

The Monocotyledons exhibit an interesting formation of the leaves. Narrow leaves with parallel nervature are given as being the characteristic leaf for this group. This leaf, though most frequent among the Monocotyledons, is not restricted to them. We find leaves of a similar structure in some Dicotyledons, e. g. in the genera *Bupleurum, Plantago, Eryngium, Ranunculus flamula,* etc. On the other hand the dicotyle structure of reticularly veined leaves is not rare among the Monocotyledons, and predominates in the dicotylophyll evolutionary group, in all the Araceae, and occurs also in many Helobiae. It is also found in the *Orchidaceae,* though relatively rarely. Both groups have thus only different ratios of the quantitative representations of these types. In broad leaves the parallel nervature passes very easily into a pennate or digitate nervature. These transitions we find in almost all broad-leaved types, and they do not seem to afford a very important criterion. Wherever a tendency to the formation of broad leaves appears, there appears also a tendency to a lesser or greater origin of pinnately or digitately venate leaves. These leaves thus belong only to the modifications of the leaves with a parallely venate nervature. As the individual types defined themselves in the invidual families they can be here quite a good criterion. Often, however, we find exceptions, which indicate that the formation of the leaf is never an absolutely firmly fixed character.

All the other characters may vary just as much as the shape of the leaves. Mostly we can know only by directly observing the material which character changes and how it changes. It is not possible to formulate too absolute rules in this connection, as organic nature may sometimes form very strange modifications. Nevertheless it is possible to observe certain regularities. Some changes are formed very easily and in different evolutionary groups, others are very rare and often characteristic only for one definite evolutionary group. Thus it depends only on a correct selection of the characters whether or not we are able to arrange the plants into conformable evolutionary taxons and at the same time to erect on these a hierarchic system according to graded relationships. This is the most important task of taxonomy. It is, however, necessary first to make sure that the principles according to which we erect the system correspond to the processes as they actually take place in nature. This is so obvious a precaution to take that it would not be worth mentioning were it not for the fact that experience shows how easy it is to over- or underestimate the value of the various criteria chosen, with the result that the ensuing system becomes totally vitiated as its very structure is false. Naturally also our conceptions of evolution as due to affinity complications of matter (in contradistinction to complications by conflicts), of the phasic evolution of the plants and the material predisposition will of course influence our erection of the taxonomic units. I give therefore here a brief summary of my view of the origin of the Monocotyledons and their differentiation into evolutionary groups.

The stock from which the Angiosperms eventually arose must have originated during the differentiation of the vascular plants, i. e. probably already in the Paleozoic. This stock continued to exist as a small number of individuals until the Mesozoic, when its re-organisation took place. This re-organisation resulted in the on the whole rapid disintegration of the stock, which gave rise almost simultaneously to several basic groups, one of which formed the Monocotyledons and the other two or three the Dicotyledons. These basic groups had a great evolutionary vigour, and thus gave rise to new shapes and properties. Thus the basic groups disintegrated at once further into new types. As, however, the evolutionary vigour gradually decreased, these types did not possess the same evolutionary capacity as their ancestors. They disintegrated thus into lower and lower taxons around certain centres of the original plastic stock. A stabilised species in the present sense of the term need not even have existed. The individuals were probably not stable and may not have preserved all the properties of their ancestors. It was only in the course of the gradual stabilisation of the evolutionary vigour that the species became stabilised in the form which we know today.

It seems that as each evolutionary group separated out certain definite types from the plastic stock in the course of the different evolutionary stages, some properties and shapes became stabilised in these types, probably corresponding to the evolutionary changes which took place in the plastic stock. The plastic stock itself did not maintain itself as such, and continued to change until the most constant predisposed types arose. It is just from those types which broke away from the evolutionary trend that we can learn the probable course of evolution. The preservation of definite evolutionary phases is a property of the whole evolution of the plants; without it we should have to trace evolution only on the basis of the fossilised remains. In order to be able to reconstruct this evolution we have to select from the present types the plants with such characters and properties which can give us an approximate idea of their evolution. The correctness of such a reconstruction can of course to some extent be controlled by comparison with the paleobotanical data.

The differentiation gave rise to groups which are characterised by definite features specific for each group. According to these common features we recognise today the members of such groups. On this basis it is possible to erect the reconstruction of the evolution of the plants and to define definite groups and their mutual relations. Although this sounds very simple, it is in reality, as experience shows, by no means easy, and one must constantly be on one's guard against making mistakes in the diagnosis of what constitutes common features. The only way in which to proceed with at any rate some insurance against a misinterpretation of the facts given is by constantly sifting and refining one's interpretations and again and again go back to the verification of all data. Hence no definite system can be reached for years to come. In the meantime, however, it is possible already at the present stage of our knowledge to arrive at a conception of the evolution of the plants which is in the main true and correct, however much it later may have to be corrected in detail.

On the basis of this conception it seems most probable that the plastic stock of the Monocotyledons disintergrated into several large centres. Each of these centres is characterised by a somewhat different evolution, as different elements developed and stabilised themselves in the various centres. Apocarpy seems to be a very important character of the Monocotyledons. When it occurs in some family, it is mostly connected also with many other characters which we regard as quite primary ones. Syncarpy on the contrary is mostly connected with a great stability of the whole structure of the flower and with the presence of characters which we regard as more derivative. In compiling the groups it was just this difference between apocarpy and syncarpy which was used as a very important criterion. The individual groups as well as the individual members of each group were compiled by proceeding from the apocarpic and monocarpic types to the syncarpic types. The evolutionary trend seems to go from apocarpy with undefined flowers to syncarpy with characteristically trimerous and pentacyclic flowers. All types which have not reached this perfection, and thus also asymmetrical, morphologically very complex flowers, are regarded as lateral lines. They broke away from the main evolutionary trend before they had reached the terminal characters predisposed in all Monocotyledons.

In the Monocotyledons eight great evolutionary groups can be observed, each with several families. Some are isolated, others show an affinity also with other groups. By its evolutionary trend the hydrophile group is linked to all groups. The spadicoid and the dicotylophyll groups stand rather alone. The graminoid group is clearly related to the xeranthemous group, and the latter in its turn is more distantly related to the sepaloid group. The sepaloid group shows certain agreements with the anomalous group. In the following chapters the individual evolutionary groups and the families forming them will be discussed.

The Hydrophile Evolutionary Group.

The hydrophile evolutionary group consists of ten families with very different evolutionary trends. They are, however, connected by some characters which might indicate affinities. Inconstant and undefined conditions in the formation of the sex organs appear in all families of this group. They indicate that the origin of this group could have taken place already in the first stages of the euryplastic phase. The structure of the flower is in some families very simple.

Lilaeaceae.

Monotypical, taxonomically very interesting family, bound to an environment with a redundance of water. Leaves linear, sheathing and ligulate. Squamulae intravaginales as minute scales. Flowers in dense spikes, most often female below, hermaphrodite in the middle, and male above. In addition to these flowers there are still exclusively female flowers growing below on the sides of the stem and enclosed in the sheath of the leaf, from which only the style, often more than 10 cm. long, projects. The flowers have no perianth and usually grow subtended by a scaly bract. The males consist only of one, two-celled anther growing in the axis of the scale. The hermaphrodite flowers are composed of the stamen and of the ovary, which stands closely above the stamen. The females consist of the ovaries subtended by a bract or without it. The ovaries are 1-celled, with one ovule. Stigma capitate, penicellate. Fruit a ribbed caryopsis.

This remarkable type seems to be systematically very important. It indicates similar evolutionary principles as we observe them in the families *Cyperaceae* and *Gramineae*. The flowers without perianth arranged in a spike and consisting of monocarp pistils and the grass-like leaves make these two groups approach each other so that it is not difficult to form an idea of their similar origin. They may represent the beginning of the differentiation leading to these two families. It is of course not possible to regard the *Lilaeaceae* as the ancestor of these families, but they had very probably common ancestors. The *Gramineae* and the *Cyperaceae* have, however, advanced much farther in their evolution, *Lilaea* thus represents a phylogenetically very important type which helps to elucidate the origin of the graminoid group.

Najadaceae.

Monogeneric family of aquatic plants. Leaves linear, apparently opposite or whorled, sheathing. Squamulae intravaginales present. The monoecious or dioecious small flowers are solitary or several together in the branch axils. The males are composed of one stamen enclosed in a spathe-like bract; the anthers are 1-4-celled. The females are composed of one ovary without perianth, or are closely enveloped by a spathe and sometimes subtended by a bract. Ovary 1-celled, of 1 carpel, with one basal ovule. Style with 1—4 stigmas. Seed without endosperm.

The position of this family is also phylogenetically very interesting. Opinions differ as to the valence of this family. Campbell's extreme view designates it as the most primitive Angiosperms starting from the heterosporic Filicales. Hutchinson's view on the contrary designates this family as an advanced type. Both these views seem, however, to be extreme. The *Najadaceae* represent the evolutionary trend of the hydrophile group, in which a similar simplification of the flowers took place as we observe it in *Lilaea*. A similar, but less radical evolution overtook also the *Gramineae* and *Cyperaceae*, where it came likewise to the formation of a 1-celled ovary. But the remaining flower parts did not remain so simple in them. The *Najadaceae* are on the whole an isolated type.

Zannichelliaceae.

Plants submerged in water. Leaves linear, sheathing and often ligulate. Flowers small, mono- or dioecious, axillary solitary or in cymes. Perianth absent or of 3 small scales, sometimes membranaceous cup-shaped. Stamens 1—2 or 3. Gynoecium of 1—9 free carpels, each with one ovule. Style 2-4-lobed. Fruiting carpels indehiscent. Seeds without endosperm.

Similar evolutionary trends show themselves in this family as in the *Najadaceae*, to which it is related; but it does not have such a strong reduction of the stamens and gynoecia. The leaves have already a grass-like character.

Lemnaceae.

Narrowly specialised group of aquatic plants with a very simple structure of the body. They consist of tiny thallus-like bodies constantly segmenting. Also the flowers have a very simple structure. They are without perianth or are enclosed in a membranaceous sheath. They consist of one to two stamens and a one-celled ovary, which carries at the base one to seven ovules. Stigma short spathulate. Seeds either without or with endosperm. Because of the lack of characters it will always be difficult to ascertain with absolute certainty the affinity of this family. Thus it is necessary to rely more on the evolutionary significance of the characters than on their shapes. Most often this group is regarded as a degenerated type of the *Araceae* and derived from the genus *Pistia*. But there is an immense leap between this genus and the family *Lemnaceae*. The evolutionary tendencies in the family *Araceae* are different, and the placing of the *Lemnaceae* in their affinity seems forced. On the other hand all the evolutionary tendencies which can be observed in the *Lemnaceae* appear also in the families of the group Helobiae. In 1945 Lawalrée (after Lawrence) discovered in the genus *Spirodella* squamulae intravaginales. Thus he confirmed the close affinity of the *Lemnaceae* and the Helobiae. The position of the stamens and gynoecia is reminiscent of many conditions in the *Lilaeaceae* and also in the *Zanichelliaceae*. The *Lemnaceae* have not only a similar structure of the stigmata, but also the pollen is rather similarly formed as in the *Zanichelliaceae*. A similar type of pollen is not known in the family *Araceae*. In the family *Araceae* and especially in *Pistia* the stamens and gynoecia are mostly more remote from each other and do not grow on the sides of the style as in the *Lemnaceae*. Also the whole habit is difficult to derive from the family *Araceae*. In the Helobiae a similar evolutionary trend can be seen in the origin of overwintering buds (hibernacula). By the modification of this ability can be explained the origin of the otherwise strange axile bodies and their segmentation. Also the fruit is nearer to the group Helobiae than to the *Araceae*. Also opposite leaves are common in the group Helobiae, whereas the leaves in the family *Araceae* are always alternate. A similar simplification of the flowers often occurs in the monocarp types of the hydrophile group. Though the *Araceae* and *Lemnaceae* are fairly closely related, yet the *Lemnaceae* do not fall outside the hydrophile group, whereas the evolution of the *Araceae* shows another trend. Also, notwithstanding the great simplification, there are here in the *Lemnaceae* great basic modifications in the configuration of the flowers in the different species. This character and the remarkable habit indicate that this family represents an extreme group formed already in the euryplastic phase. It belongs to the dispersion of the hydrophile group. Thus it seems that though the *Araceae* and the *Lemnaceae* are related, yet it is more probable that the *Lemnaceae* never had types with a spadix as ancestors. Thus it is not possible to derive them from the *Araceae* either. The two families are of different evolutionary tendencies.

Potamogetonaceae (incl. *Ruppiaceae, Zosteraceae, Possidoniaceae*).

Aquatic plants with linear to broad, often reticularly veined, sometimes also ligulate leaves. Squamulae intravaginales developed. Flowers hermaphrodite, one- or two-oecious, in spikes growing from showy bracts. Perianth undifferentiated, of 4—6 segments, stamens 1—4, gynoecium of 4 carpels, 1-celled, with one ovule. Seeds without endosperm. Here belong the genera *Potamogeton, Ruppia, Zostera, Phyllospadix* and *Posidonia.*

This family represents probably a lateral evolutionary group in which many characters have been preserved which indicate a close affinity with the other families of the group. Here a similar evolutionary trend made itself felt as in the *Araceae.* Spathe, spadix, bisexuality, unisexuality, small flowers, varying number of flower parts, nondeveloped endosperm, etc. are indicated here. The undefined conditions in the flower parts indicate an origin in the euryplastic phase. It is not excluded that there appear here some characters which the precursors of the Angiosperms possessed. Especially the structure of the flower, sometimes interpreted as inflorescence, indicates primitive conditions.

Aponogetonaceae.

Explicitly aquatic plants, leaves reticulately veined. Flowers bisexual, rarely unisexual, in spikes, without perianth, or with one to three petaloid segments, only rarely a membranaceous bract. Stamens 6 or more, free. Gynoecium of 3—6, free carpels. Ovules two or more, basal, anatrophous. Seeds without endosperm.

Monogeneric family with a simple perianth or with flowers without perianth. It is presumably a lateral evolutionary group in which some inconstant conditions appear. On the whole it shows, however, already a stabilisation of the evolutionary vigour.

Scheuchzeriaceae (incl. Juncaginaceae).

Family bound to an environment with a redundance of water. Leaves linear, sheathing, ligualte. Squamulae intravaginales as minute scales or hairs. Flower hermaphrodite, unisexual, or polygamous. Perianth undifferentiated, in two trimerous, rarely tetramerous *(Tetroncium)* series, rarely only 3 in one series. Carpels 3—6, weakly connate at the base. Stigmata sessile, papillose or plumose. Ovules 2 or several, basal, erect, anatropous. Seeds without endosperm.

Though the variation of the flower segments is smaller in this family, yet it is still rather considerable. The leaves have a very uniform, linear shape. Squamulae intravaginales, apocarpous gyneocia and the varying conditions indicate that this family originated in an early euryplastic phase. It shows also affinity to the other families of the group. The division of this family into two separate families does not seem justified. The differences are not very essential. In the euryplastic phase when these types were formed there could be considerable differences also in closely related types. The inconspicuous flowers and the grass-like character indicate an affinity to the graminoid group. It is, however, not excluded that there is an affinity to some genera of the fam. *Liliaceae* as e. g. to the genus *Tofieldia* etc., distinguished only by the more stabilised structure of the flowers.

Butomaceae.

Marsh or aquatic plants. Leaves linear, below trimetrous, above ensiform. Flowers in apparent umbels. They are of a fairly stabilised type, actinomorphic, hermaphrodite. Calyx and corolla trimerous, persistent. Stamens in two series, by 6—3. Gynoecia of 6 free carpels.

All the genera of this family were transfered to the family *Alismaceae* except the one genus *Butomus*. In justification of this division one referred to the macromorphology as well as to the shape of the pollen. By the morphology of the flowers also this genus belongs, however, to the affinity of the *Alismaceae*, but it represents its more isolated, more distantly related type.

Alismaceae.

Family closely bound to an aquatic environment. Leaves variable in shape, linear to broad, reticulately veined. Squamulae intravaginales present. Flowers hermaphrodite, unisexual to polygamous. Calyx and corolla differentiated, corolla rarely lacking *(Burnatia, Wiesneria)*, or the calyx is coloured. The number of stamens varies greatly, between 6 and many, rarely there are only three *(Wiesneria)*. Also the number of carpels varies considerably in the individual genera, from 6 to many. They are superior and free, only in the genus *Damasonium* they cohere at the base only. They are arranged in spirals or in whorls. Ovules anatropous, one to several. Seeds without endosperm. The unstabilised numbers of the stamens, carpels, ovules, the apocarpous gynoecia, the distribution throughout the world, the resemblance to the Ranalian taxa indicate that the family originated still at the time of unstabilised evolutionary vigour. Probably by the influence of the aquatic environment also some characters of the ancestors of the Angiosperms have been preserved here. The differentiation of the perianth into calyx and corolla indicates the affinity to the sepaloid group. The rarely occurring coloured calyx gives the possibility of relationship also with the tepaloid group, and especially with the family *Pontederiaceae*. There are here, however, also probable relations to families of the dicotylophyll and anomalous group (via the *Triuridaceae* and *Trilliaceae*).

Hydrocharitaceae.

Family bound to an aquatic environment. Leaves very variable, linear and broad, reticulately veined, alternate, whorled or opposite. Spathe of one to two bracts, squamulae intravaginales at the base of the leaves. Flowers bisexual to dioecious. Heterogamous flowers are usually different. Several males are together in spathes, the female is solitary. We observe such different manifestations of sex dimorphism also in other taxons, and they indicate a different morphogenous action of the different sexes. Calyx and corolla differentiated, mostly trimerous, the corolla only sometimes lacking. The number of stamens varies between one and many, and they are arranged in one to five series. Gynoecium inferior, of 3—15 carpels, connate, 1-celled. Style one, with one stigma, or the number of stigmas agrees with the number of placentas. Stigmas often two- to three-lobed *(Egeria)*. Seeds numerous, without endosperm.

The great variability of the individual genera in the leaves and flower parts and further the world-wide distribution indicate an origin in the euryplastic phase. Gynoecium inferior, sometimes connate only at the base. Thus there appears here a basic evolutionary trend characteristic also for some very stabilised families. The individual 2- to 3-lobed styles indicate that the relation of the number of branches to the number of carpels is doubtful. As a very extreme character the squamulae intravaginales link this family to the affinity of the remaining families of this group. It seems that this family may represent an evolutionary centre around which a great number of stabilised types formed. The differentiation of calyx and corolla is in common with the sepaloid group. This family shows clearly that an inferior syncarpous gynoecium could form already at the beginning of the euryplastic phase.

Summary: The hydrophile evolutionary group represents a group in which all basic characters of the other evolutionary groups are developed. The affinity of this group can be seen from some extreme characters which the members of this group have in common, and which elsewhere we do not observe at all or only very rarely. In this group we find species with the most different basic structure. There are here representatives with the perianth differentiated into calyx and corolla, with an undifferentiated perianth, types with spathelike bracts, types with a spadix, connate and free gynoecium, cyclic to spiral arrangement of the flower parts, types of a grass-like aspect, types with a dicotyle structure of the leaves etc. On the other hand the affinity of all these morphologically so different types is clear from the presence of squamulae intravaginales, which are developed in most of the genera, and further from the absent or weakly developed endosperm in the seed, and finally also from the similar ecology. We find, however, a non-development of an endosperm also in some other aquatic plants, and thus it is not excluded that this character may be to some extent connected with the aquatic environment.

The evolution of this group took quite a different course than in the other groups. The whole group disintegrated into a series leading from the most simply built flowers without perianth via types with a superior gynoecium to inferior gynoecia and trimerous, pentacyclic flowers. Though a tendency to the formation of trimerous flowers is visible, there are also many deviations. In the other evolutionary groups evolution led mostly to a quick stabilisation of the structure of the flower and of the vegetative parts. The changes took place in them mostly in a rich combination of more subordinate characters. In the hydrophile group there was variation in the basic characters, but the number of types formed and preserved is not great. Only the family *Potamogetonaceae* attained more than a hundred species. This is a very small number as compared with the other large families. We see in this group some indications very important for the phylogenetic valuation of the other groups. Thus the *Gramineae* and *Cyperaceae* are often considered to be indistinctly threecarpelic, and as reason for this view are given the three-branched stigmas or three independent stigmas. This, however, sometimes does not apply in the group Helobiae, and we see that often also a one-carpelic gynoecium bears two to four stigmas *(Najas, Phyllospadix)*, or also that though a syncarpic gynoecium has stigmas in the same number as carpels, yet each stigma is still two-to three-lobed *(Anacharis, Egeria)*. Thus the stigma branches or stigmas need not always indicate the number of carpels. The significance of this character may thus be twofold also in the other groups. Either it agrees with the number of carpels *(Liliaceae, Amaryllidaceae)*, or it does not and corresponds only to the stigma branches *(Cyperaceae, Gramineae)*.

The origin of this group obviously took place at a time of great evolutionary vigour, as the types preserved indicate unstabilised conditions. The characters stabilised in this family thus seem to indicate types which quickly preserved themselves already in the first evolutionary expansion. In view of the favourably stabilised ecology they have been able to maintain themselves to this day. We observe here all the basic modifications of the flowers from the most simple ones restricted to the stamen without perianth or to the naked ovary via trimerous and pentacyclic types to types with an undefined number of members and series. Thus it is tempting to derive all other Monocotyledons from this group. It looks as if these types had departed from the initial formation of the main evolutionary group and stabilised themselves with evolutionary characters of different values. If this is so, then the question arises whether this group is at all based on direct relationship or whether it embraces the types dependent on an aquatic environment and belonging to the different main evolutionary groups.

Thus in the hydrophile group the basic types are developed which we observe also in the other groups of the Monocotyledons. These groups can thus be derived from these basic types. This cannot be done in any other group of the Monocotyledons. Even the *Liliaceae,* which are often regarded as the evolutionary centre of the other Monocotyledons, do not make it possible for us to derive all other groups from them without rather wrenching the evidence by disregarding great gaps between them. It is difficult to imagine an evolution of the family *Liliaceae* running to monocarpy and to flowers without perianths. Also the origin of the great variability of the characters in some other families is difficult to assume from so stabilised types as are the *Liliaceae.* The groups which include types with apocarpous gyneocium are in most cases connected also with a greater total variability of the basic characters. Thus they must have originated at an earlier time, when the evolutionary vigour was not yet stabilised. Thus it is necessary to regard them as more primary than the types which are very constant. It seems that one far too often regards reduction as a deus ex machina. If reduction were so all powerful, then it would be far more frequent in nature than evolutionary progress, but it is difficult to imagine that it was so very frequent a phenomenon. Mostly such regressions as we have can be interpreted quite well as progressive evolutionary stages of the groups which became very quickly stabilised and originated already in the formation of the higher taxons in the euryplastic phase. An evolution leading from perfectly developed types to simplified ones may have been frequent, but such a simplification is easily recognised; at least in some genera or species it comes in it to the stabilisation of the normal types or to the preservation of rudimentary organs.

Good examples are offered by the *Scitamineae* and *Orchidaceae.* Where no traces of former organs have been preserved it is more likely that the simplification is only apparent, and that in reality there was a stabilisation of certain evolutionary stages of progressive evolution. It is not necessary to assume that the evolution of the simple types went always via ancestors with perfectly developed pentacyclic trimerous flowers.

The family *Pontederiaceae* seems to be very closely related to this group, and can even be placed directly in the hydrophile evolutionary group. Its ecological character, morphological structure of the flowers and of the vegetative parts show a similar evolutionary trend as that in the hydrophile group. The evolution of the *Liliaceae* can be imagined to have gone via this family, nor is it difficult to link up most of the other evolutionary groups with the hydrophile group. The *Hydrocharitaceae, Alismaceae* and *Butomaceae* link up naturally with the sepaloid and dicotylophyll groups, the *Alismaceae* and *Butomaceae* also with the anomalous group. The *Liliaceae* link up with the graminoid group, and the *Potamogetonaceae* with the spadicifloric group.

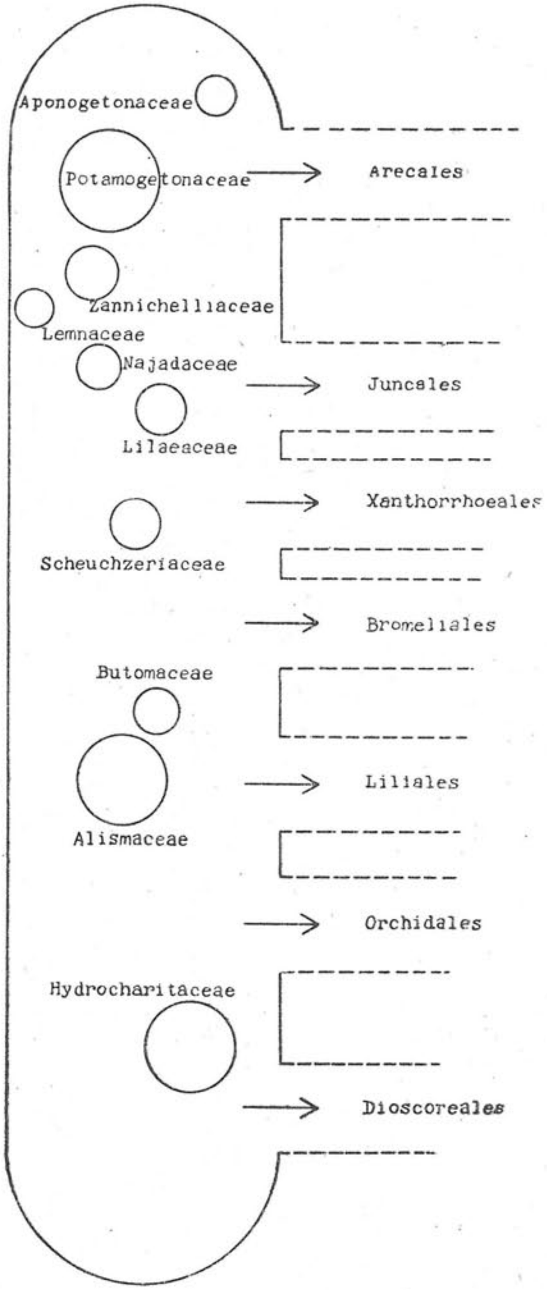


Fig. 1. — Representation of the relationships of the *Helobiae* to the other evolutionary groups of the Monocotyledons. The large ellipse indicates the group *Helobiae* and the circles within it represent the families differentiated in this group. The arrows from a certain area within the ellipse indicate the probable affinity with the other evolutionary groups of the Monocotyledons.

The Spadicifloric Evolutionary Group.

Though the spadicifloric evolutionary group shows a similar evolutionary trend in all families, yet the evolution took a rather different course in the individual families, so that the relationships are often not striking. This group consists of seven families characterised by a striking type of inflorescence. The common characters are spadix and spathe. The structure of the flower is very unstabilised in most families.

Araceae.

Terrestrial marsh plants, rarely also aquatic plants *(Cryptocoryne, Pistia)*. Leaves of very different shapes, most often with broad blades, often divided and mostly reticulately veined. The flowers grow on the spadices supported by a spathe. The structure of the flowers differs greatly. They are hermaphrodite, unisexual, small, dimerous or trimerous. A perianth is sometimes developed in the hermaphrodite flowers, and is composed of 4 to 6, rarely 7—9 segments, sometimes connate. In the unisexual flowers it is mostly absent. There are 5—8 stamens behind the perianth segments. In some types the filaments of the stamens are joined together. Gynoecium superior or immersed in the spadix. It is most often tricarpelic, more rarely 1-, 2- to 9-carpelic. In each compartment are one to many ovules. Their placentation is basal, parietal, axile, or apical. The fruit is most often a berry. The seeds have most often an endosperm, rarely the latter is not developed.

This family is mostly explained as derived from the family *Liliaceae*. This view is based on the assumption that the basic initial flower was pentacyclic and trimerous (Hutchinson). It seems, however, that such a flower is rather the predisposed terminal stage than the initial stage. This family is very interesting phylogenetically. The variations in the flower parts are so far-reaching that hardly anything like it can be found among the Monocotyledons. Already this indicates an ancient type, which cannot be derived from an almost stabilised family such as the *Liliaceae, Palmae,* etc. A similar variability is found in the family *Potamogetonaceae* with which they have many characters in common. Also in this family we find one- to many-carpelic gynoecia, a perianth or also flowers without perianth, one to many stamens, flowers 1-, 2-, 3-merous, leaves reticulately veined, spadix, spathe, small flowers, perianth free or connate, seeds without endosperm, etc. But the aroids go still further as also ligneous types occur in them, they have a wider ecological amplitude, a more complicated anatomic structure, entomophily is developed, they have an endosperm, a more complicated structure of the leaves and inflorescence, etc. All these properties indicate that the species originated in the euryplastic phase, and thus it cannot be an advanced family. This is also indicated by the paleobotanical evidence, for the *Araceae* belong to the first Monocotyledons. It seems, however, that we have to separate from the *Araceae* the genera *Acorus* and *Gymnostachys* with linear leaves, which show not only a biological but also a morphological affinity to the family *Sparganiaceae* (especially the second genus). Both these families are attacked by a specific rust, as ascertained by Parmelee and Savile (Life-history and Relationship of the Rust of *Sparganium* and *Acorus:* Mycology 46, 823—36 1954). The authors arrive at the conclusion that the two genera are far more closely related than was thought up till now. The quite exceptional position of the genera *Acorus* and *Gymnostachys* in the family *Araceae* indicates a higher taxonomic valence of these two genera. They form a transition group between the *Araceae* and the *Sparganiaceae*. Especially the genus *Gymnostachys* is evolutionarily close to the fam. *Sparganiaceae*. It may thus be justifiable to separate these two genera from the remaining family *Araceae*. It is probably a separate family on the transition between the *Araceae* and the *Sparganniaceae*. They have common ancestors, but it is not possible to derive the one from the other. The parallel-veined leaves, undifferentiated spathe, perfectly pentacyclic flowers, orthotropous ovule, distichous leaves, all form an alien evolutionary element among the *Araceae*. It is an ancient group, distributed in both hemispheres, but only in three species in all.

Pandanaceae.

Trees or shrubs with aerial roots. Leaves parallel-veined, closely crowded, spiral, often in 2—4 rows screw-like turned. Flowers dioecious in panicles or into spadices enclosed by green or coloured spatheceous bracts. Perianth rudimentary or absent. The remaining flower parts have an unstabilised number of members, often in great numbers. There are usually many stamens, sometimes variously connate. Gynoecium superior, one to many, 1-celled. Fruit syncarps. Ovule anatropous, one to many in each cell. Seeds tiny, with endosperm.

This family is very interesting from an evolutionary point of view. Most often it is regarded as related to the family *Sparganiaceae,* with which it has many characters in common, such as the inflorescence, the cohering of the carpels (in the genus *Sparganium* this occurs as abnormality), cohering of the stamens, parallel nerves of the leaves, ecological character, etc. J. Velenovský regards the *Pandanaceae* as the ligneous parallel of the *Sparganiaceae,* as it is often the case also in other pairs, e. g. in the Monocotyledons the *Liliaceae—Agavaceae,* or in the Dicotyledons the *Ranunculaceae—Magnoliaceae, Cruciferae—Capparidaceae, Umbelliflorae—Araliaceae,* etc. The evolutionary changes which we observe in the two families show a considerable similarity. It is not excluded that both families had common ancestors. Today, however, they are rather isolated families, which show more remote relations also to the families *Typhaceae, Cyclanthaceae, Palmae.* Simple perianth indefinite number of stamens, carpels, ovules, apo- and syncarpous gynoecium, wide distribution, occurrence already in the Lower Cretaceous indicate that this family originated very early in the differentiation of the Angiosperms.

Sparganiaceae.

Aquatic and marsh plants with linear, distichous leaves and with ranks often turning screw-like. Flowers unisexual, in clusters. Perianth most often as three scales, rarely one to six scales, or also entirely absent. The male flowers have three or more stamens. Female with superior gynoecium, 1-celled, of one, rarely of two carpels. One ovule in each. Style simple, or divided. Fruit nutlike with spongy exocarp and hard endocarp. Endosperm mealy.

Monogeneric family. Phylogenetically it seems to belong to the simply built Monocotyledons as a parallel evolutionary group of the families *Typhaceae* and *Pandanaceae*. It shows also some relations to the *Araceae* and especially to the *Acoraceae*. The unstabilised conditions indicate an origin in the euryplastic phase. But the family soon became stabilised evolutionarily and is restricted to one genus only.

Typhaceae.

Aquatic and marsh plants with linear leaves. Flowers unisexual, very small, in a dense terminal spadix. They have a very simple structure. Perianth absent. Male composed of 3, more rarely of 2 to 7 stamens. Filaments free or united, with long hair at the base. Female flowers often subtended by an axial bract. They are formed by a 1-carpelled, stipitate superior ovary, on a stipe bearing silky hairs. The female flowers often grow from an axial membranaceous scale. The carpels contain one ovule, and in the fruit turns into a nutlet or caryopsis. The seeds have a mealy endosperm.

It comprises only the one genus *Typha*. It shows affinity to the family *Sparganiaceae*, and remotely also to some monocarpelled Monocotyledons *(Gramineae, Liliaceae)*. Notwithstanding the small number of species formed the great variability of the characters indicates an origin in the euryplastic phase. But the family soon became stabilised in its evolution.

Cyclanthaceae.

Herbs or shrubs similar to the palms. Sometimes juices are developed as in the *Araceae*. Flowers unisexual, closely crowded into a spadix. Several male flowers grow around one female flower, or the flowers are arranged in alternating male and female whorls. Spadix in youth enclosed in caducous spathes. The male flowers have a cuplike perianth or are without perianth, with numerous stamens, often variously connate. Females without perianth, or as 4 free or connate segments. They have usually 4 staminodes. Ovary superior or sunk into the spadix, 1-celled, with 1—4 carpels, with 1—4 stigmas. Ovules numerous. Fruit a fleshy syncarp of connate or separate berries. Seeds with endosperm.

Taxonomically a very remarkable family. Morphologically it is somewhat isolated as rather extreme characters stabilised themselves in it. Most often the family is regarded as an advanced derivation of the palms, or as standing between the palms, aroids and pandanus. Especially in the first two families we can observe a similar evolutionary trend as in the *Cyclanthaceae*. Here a whole number of evolutionary characters common to the whole group is developed. The origin of this family cannot, however, be derived from the relatively more stabilised *Palmae*. In the *Cyclanthaceae* one can observe a number of very simple characters, but also very complex characters. No similar morphological structure is developed in any other group. Thus it is probable that this family differentiated itself already from the primary plastic stock of the group. It represents a quickly developing and soon stabilised family. Some characters occurring in this family can elucidate the basic processes which we observe in the formation of the flowers. The difference between flower and inflorescence is here considerably effaced. It is not difficult to imagine that the spadix could turn into a simple flower. The coloured caducous spathes, the reduction of the superposed whorls of male and female organs to two series could easily form a flower. It is not excluded that this phenomenon, which we observe also in many other primitive groups, as in the other Monocotyledons with spadix and in the *Potamogetonaceae,* may indicate a primitive property of the ancestors of the Angiosperms. The frequent syncarp of the whole inflorescence indicates the evolutionary unity of this organ. It is easy to derive in a similar way the simple flowers from composite sporangia. In the *Cyclanthaceae* there is still one remarkable phenomenon: The simple, but perfectly differentiated female flower is surrounded on the spadix by a number of male flowers and all together form a whole. In this phenomenon, too, which we can observe also in the family *Araceae,* it is possible to see a tendency which indicates similar forces as those which could form the flower from the sporangia. When we accept the individual flower parts as branches of the sporangium, then there is nothing strange in e. g. such simple axile stamens or ovaries turning into a whole flower or also into an inflorescence, or, vice versa, a whole inflorescence simplifying into one stamen or ovary. What matters here is only the materially conditioned morphogenous force, which forms the flower. If this conception is correct, then it shows that the flower organs originated from the axis and not from the leaves.

The undefined number of the flower parts, the tendency to flower dimery, without perianth or with simple perianth, the strangely differentiated spadix indicate a great evolutionary vigour, which became fixed here. The small area of the family is, however, remarkable; it may have been due to the evolutionary vigour having been lost early rather than to the family having originated late. The loss of the evolutionary vigour involved an inability to overcome obstacles by the formation of suitably adapted types. The area of the family belongs, however, to the region in which we have placed the origin of the Angiosperms. Thus we have here probably a primitive family, in which, however, some extreme characters manifested themselves.

Palmae.

Trees of a rather uniform though unusual aspect. Leaves large, digitately or pinnately veined, sheathing, often ligulate. Flowers small, in simple or paniculate spadices. The flower parts are most often trimerous and pentacyclic, and are already rather stabilised. For the rest, however, a considerable manifoldness developed, and we find here hermaphrodite as well as monoecious or dioecious types, and rarely also polygamous ones. A multiplication of the stamens is not rare. Ovaries apo- or syncarpous, 3 carpels, rarely only one to two carpels *(Caryota, Sclerosperma, Didymosperma).* Ovules single. There is a great diversity in the organisation of the fruits, which have often pericarpium and testa differentiated into several modified layers.

Taxonomically this family is fairly closely related in the vegetative as well as in the generative organs. Only *Phytelephas* and *Nipa* deviate, and have a different number of flower organs. In *Phytelephas* the flowers are mostly dimerous, and the number of carpels and stamens varies. In *Nipa* they are trimerous, females without perianth, males with connate stamens. In these two genera similar evolutionary tendencies show themselves as in the *Pandanaceae* and *Cyclanthaceae* (great number of stamens with rudimentary or absent perianth, connate stamens, indefinite number of carpels, syncarpium). Thus the *Palmae* show an obviously similar evolution as the families *Pandanaceae* and *Cyclanthaceae.* It is possible to regard them as an evolutionarily homogeneous group. They show also a more remote evolutionary resemblance to the other members of this group. The evolution of the palms and their differentiation are, however, a little simpler than in the preceding groups. Nevertheless symptoms of unstabilised conditions are to be found also here, although they are rather only exceptions occurring in some genera. Most of the modifications are qualitatively fairly uniform. The wide distribution and often disjunctive areas indicate a great age. Hutchinson derived this family from some genera of the family *Agavaceae.* The apocarpous gynoecium, the differentiated perianth, the far greater variation in the basic organs do not indicate an advancement from a stabilised family, but rather ancient conditions. The palms as mostly ligneous types probably quickly stabilised themselves evolutionarily. They have preserved many characters from the euryplastic phase when the evolutionary vigour was subject to great oscillations. The basic type became, however, soon stabilised. Later there arose here probably new evolutionary possibilities, but these led only to a disintegration into many lower taxons, mostly genera and species.

Summary: This evolutionary group shows a number of morphologically rather different types. All are, however, connected by a similar evolutionary trend. No orthogenetic lines appear here leading to a definite, more or less complicated type. The modifications of the individual families have different directions, and obviously centre in a basic type which is best defined by the type of the inflorescence; the other parts, though varying only within a certain range, vary already far more in the individual families and often differ even radically. In all families of the group one can find common evolutionary elements due to a parallel and related evolution. Just by these relations all families are connected into one group. It is here possible e. g. to distinguish three types according to the different formation of the leaves: sparganoid, aroid and palmoid, which developed on the whole independently.

In some genera of the hydrophile group we observe an evolutionary trend which is similar to that in the spadicifloric group. Especially the *Potamogetonaceae,* though habitually very different, have a similar evolution of the basic organs (inconspicuous flowers, simplification of the structure of the flower, apetal types, bracts under the inflorescence, superior gynoecia, apocarpy, leaves sometimes ligulate, sheathing, dicotyle nerves of the leaves, undefined conditions of the flower parts, spadicoid inflorescence, etc.). Except for not too close relations to the hydrophile group the spadicifloric group stands apart from all remaining families. Thus it forms a rather isolated group in which mostly another evolutionary trend manifested itself than in the remaining Monocotyledons.

All families of the group did not have the same evolutionary vigour, and some became soon stabilised and did not disintegrate into numerous modifications. Such types are the *Typhaceae, Sparganiaceae, Pandanaceae, Cyclanthaceae,* and *Acoraceae.* The others obviously retained their evolutionary vigour for a long time so that they underwent also a strong evolution in the meso-evolutionary period, when a favourable reorganisation of the evolutionary possibilities led to the rise of many similar genera and species. This shows itself especially strongly in the palms, where some 210 genera and more than 4000 species were formed, yet there are only some six to eight basic types, which probably owe their origin to macro-evolutionary processes. Thus the greatest expansion of the family was caused by meso-evolutionary processes. The second family, the *Araceae,* has only 105 genera and some 1500 species, but 17 to 27 basic types. There are here both herbaceous and woody types. This probably caused the great expansion as compared with that of the mostly woody palms. Woody types have usually an accelerated evolution, i. e. a quick aging of the evolutionary vigour, which results in a far smaller number of basic types. In this group, as in some other Monocotyledons, it is possible to observe that in the woody types pentacyclic, most often trimerous flowers predominate *(Pothoeae, Palmae).* An exception is formed by the *Pandanaceae* and the *Cyclanthaceae* with an unstabilised structure of the flower.

The Graminoid Evolutionary Group.

The common characters of the graminoid evolutionary group are the inconspicuous flowers and the grass-like leaves, sometimes reduced to sheathing bracts. The basic evolutionary trend seems to be the gradually increasing complication of the monocarpellate types via apocarpellate to syncarpellate trimerous types.

Gramineae.

Plants rarely woody, with a very uniform structure of the vegetative and generative organs. Leaves sheathing, ligulate, parallel veined. Transitions to pinnately veined leaves *(Pharus)* or digitately veined leaves *(Zeugites, Streptochaeta)* are rare. Stems noded. Inflorescence and flowers of a very characteristic and stabilised structure. The flowers of the *Gramineae* are most often explained as reduced flowers of the *Liliaceae,* and the bracts enclosing the flowers as outer, the lodicules as inner perianth. This interpretation is accepted by those who derive the Monocotyledons from the *Liliaceae,* but if it were correct, then reduction would be the main evolutionary principle. It seems, however, more probable that the evolution of most of the Monocotyledons did not take a regressive course from pentacyclic, syncarpic, trimerous flowers to flowers of fewer series, apocarpic to monocarpic. A gradual building up and complication of the structure of the flowers is more probable than a mere reduction. This can be seen also from the fact that with apocarpy a lower number of series and dimery in the flowers are connected a strong variability of the whole structure, number of members in the series, and a multitude of basic types. Therefore it seems that such types represent the more primary disintegration period of the macro-evolutionary processes. The stabilisation of the series, trimery and syncarpy signify an evolutionary quietening and on the whole more uniform basic organs. The modifications of such types concern mostly only the quantitative characters, not the qualitative ones as in the modifications originating in the euryplastic phase. Thus it is difficult to imagine an evolution from the stabilised conditions in the family *Liliaceae* to the very unstable conditions in the family *Gramineae*. Here the flower parts vary greatly in number according to the genera, and thus it is difficult to imagine that they would be in series. The parts enclosing the flower retain mostly the same distichous arrangement as the leaves. The number of glumes, lemnas and paleas varies fairly much in the individual genera. It is very probable that the two-keeled palea is not formed by the concrescence of two parts, but only by the pressure of the adjoining axis, just as in the very similar two-keeled bracts of the family *Iridaceae*. In the terminal flowers, where the palea does not fit close to the axis, it also often becomes one-keeled. Also the position of the lodicules, which are always two close together, indicates a common origin and later division as this is sometimes the case in the palea. They thus correspond again rather to bracts than to flower parts. The third lodicule is in an opposite position to the first two. The interpretation of lemna, palea and lodicules as perianth thus seems to be rather forced, and caused only by the conception that they originated from the normal flower of the *Liliaceae*. Hackel's conception, on the contrary, that there are in the *Gramineae* flowers without perianth, covered only by bracts, is far more probable and gives better the position and origin of this family. The loss of the lodicules and their multiplication can be explained far better by their variation as enclosing parts of the flowers than by a reduction of the perianth parts, which vary far less. Also the instability of the stamens varying between one and six, and only rarely many *(Pariana)* corresponds far more to the group Helobiae than to the family *Liliaceae*.

The ovaries and their morphological interpretation are very important. The ovaries of the *Gramineae* have one ovule, and are interpreted as monocarpellate or tricarpellate with a reduction of the ovules to one. One assumes tricarpellate ovaries because of the number of stigmas or of their branches. Their most frequent number is 2 to 3. Recently also E. Belk (according to Lawrence) arrived at a similar view; on the basis of anatomical investigations he ascertained "the gynoecium to be fundamentally a tricarpellate organ with 3 carpels joined edge to edge, and the single ovule of the ovary always to be attached to the posterior wall of the single locul". Nevertheless it is not possible to regard the tricarpellate gynoecium as fully proved. There are certain facts which do not speak for this. Academician Cicin showed in a lecture in Prague his results with the hybridisation of *Triticum vulgare* with *Elymus arenarius* and of *Triticum vulgare* with *Agropyrum glaucum*. In some of these hybrids it came to the formation of more caryopses in one spike. The caryopses were connected at the base, and either three of them were almost equally developed, or one was large and the other two rudimentary; or finally there grew two caryopses, of which one was sometimes rudimentary. This feature proved sometimes hereditarily stable and suitable for further selection. Phylogenetically this is a very interesting case, but for a correct evaluation one would need also data on the other flower parts. Yet even so this case seems to speak in favour of a 1-carpellate gynoecium of the *Gramineae*. By remote hybridisation there obviously appeared an either atavistic or perhaps also progressive character in the gynoecium. If the caryopsis was composed of three carpels, of which only one would bear an ovule, ovules would probably most easily originate also in the other two carpels. Thus a fruit with three embryos would result. This would thus be the most frequent case as we observe it in similar cases in other genera with syncarp gynoecia. A caryopsis forms only in genera which have a monocarp gynoecium as e. g. *Lilaea* or sometimes in the genus *Typha*. This too speaks for placing the *Gramineae* in the affinity of these types. The occurrence of two to three caryopses in one flower is similar to that in some apocarpic palms, where it also comes often to the reduction of one to two carpels and the fruit becomes apparently monocarpic. The anomalous apocarpy of the hybrid grasses thus speaks for a monocarpellism of the grasses, which has perfectly preserved itself evolutionarily. This is also confirmed by another case in the sort *Prunus avium* reported by Academician B. Němec. This sort is cultivated in the Botanical Gardens in Prague. In it there form from one flower up to 5 separate monocarpellate fruits; this agrees completely with the monocarpellism and pentacyclicity of this species. The evolutionary tendency was set free in this species probably also by hybridisation. Both cases indicate how often experimental botany could supply important evidence for the morphological valuation of characters by observing genetic processes. In them sometimes extraordinary characters may appear which are based on the setting free of evolutionary tendencies otherwise firmly stabilised.

The most frequent proof given of a three-carpellate gynoecium of the *Gramineae* is the number of the stigmata or of their branches. This is, however, no proof at all. It is true that in the syncarpic types as the last trace of the increasing syncarpy this shows itself by free stigma branches which correspond to the number of carpels from which the gynoecium originated. But this is not invariably so. Just in the 1-carpellate gynoecia we know of frequent cases of stigmata which furcate into two to three branches as e. g. in the genera *Najas, Phylospadix, Zostera, Cymodocea,* and in *Possidonia australis*. Also in some types with connate syncarpous gynoecia the stigmata correspond in number to the carpels, but are nevertheless two- to three-branched *(Anacharis, Egeria,* etc.). Thus the branches of the stigmata and also the number of the stigmata need not indicate the number of carpels. Just in the monocarpellate types this feature seems to be very characteristic. The frequent occurrence of two- to three-branched stigmata in the *Gramineae* and *Cyperaceae* speaks for a character formed in the euryplastic phase of the apocarpous types on one monocarpellate gynoecium. Otherwise we should have e. g. in the *Gramineae* mono-, di- and tricarpellate types. The number of stigma branches is, however, not essential in the *Gramineae* and *Cyperaceae,* and often we find even in one genus two- and three-branched types. Thus it is obviously a character of subordinate significance. Its variation corresponds rather to a variation of the number of branches in monocarpellate gynoecia than to a variation of the number of carpels. The number of carpels is mostly a very stabilised character. From all the reasons given above it follows that the flower of the family *Gramineae* is without perianth and monocarpellate. Thus it is a character occurring in the simplest Monocotyledons. This explains also the considerable variation in the number of stamens and bracts enclosing the flower, for apocarpy is often connected with these characters. Thus the *Gramineae* originated very early in the euryplastic phase as is also shown by their early occurrence ascertained paleobotanically. On the whole, however, the evolution of some characters became soon stabilised. Such characters are just monocarpy, the characteristic type of inflorescence, and the structure of the stem. The strong evolutionary vigour manifested itself, however, by the formation of a great number of types. All properties shown indicate an origin in the euryplastic phase and a rich disintegration in the stenoplastic phase.

Cyperaceae.

Group of plants of a grass-like aspect, growing most often in moist habitats. Leaves grass-like, sheathing, sometimes also ligulate. Stems often noded. Flowers inconspicuous, bisexual or unisexual, arranged in spikes. The spikes are rarely subtended by coloured bracts. The flower grows in an axial membranaceous bract. The perianth is only bristles or scales, very rarely somewhat coloured *(Oreobolus).* It is in two series, mostly by three, or it is absent. Stamens one to 6, most often 3, rarely up to 20 *(Evandra).* Gynoecium one, superior, sometimes enclosed in a bract, 1-celled, with one basal straight anatropous ovule. Stigmas 2- to 3-branched. Fruit nutlike. In the types with two-branched stigmas the nutlike fruits are usually flattened, in the types with three-branched stigmas 3-sided. Seeds with endosperm.

Fairly often another origin is assumed for the *Cyperaceae* than for the *Gramineae.* The *Cyperaceae* are derived via the *Juncaceae* from the *Liliaceae*, whereas the *Gramineae* are derived via the *Restionaceae* from the *Commelinaceae.* The trend of evolution in the *Cyperaceae* and *Gramineae* is, however, very similar. The valuation by the authors who regard both families as closely related is thus far more adequate. It seems that the conception of a derivation of most of the Monocotyledons from the *Liliaceae* has considerably complicated the whole system. It is more probable that the gradual complication of the types comes to an end just with the pentacyclic, trimerous types with syncarpic ovaries. This type seems to represent the predisposed type to which the evolution of the Monocotyledons was directed, and which is reached in many cases. A true reduction was probably rare in macro-evolution, and more often in micro-evolution. In the family *Cyperaceae* and also in the *Gramineae* we observe a similar basic evolutionary trend as in the families *Lilaeaceae* and *Najadaceae*. In all of them the monocarpellaty of the gynoecium is characteristically developed, but in all there is a differentiation in the formation of the androecium and perianth.

Whereas in the *Lilaeaceae, Najadaceae,* and *Gramineae* no perianth was developed, the *Cyperaceae* show a tendency to the formation of a scaly or bristly perianth. In some types it is still completely absent. It is possible to conclude to the evolution of this group from the relations of the *Cyperaceae* and *Gramineae* to *Lilaea scilloides*. The derivation of the genus *Carex* from *Lilaea* is not difficult. In both the gynoecium or stamens grow in the acillary bracts and form a flower without perianth. These flowers are arranged into spikes. In the *Cyperaceae,* however, evolution advanced further, to the formation of a primitive perianth and androecium with a different number of stamens. In both we observe most often an arrangement into trimerous series. Here a predisposed evolutionary trend of the Monocotyledons came to the fore. But the monocarpellaty was evolutionarily so stabilised that it did not develop further.

The evolution of the *Gramineae* shows a somewhat different trend. They may have arisen from similar primary types as *Lilaea,* but forming ramified spikes in which the inferior supporting bracts remained sterile and were arranged into characteristic spikelets. It was only above the uppermost ones, which were mostly developed as lodicules, that flowers without perianth developed in their axile. Thus it is possible to derive them from the middle parts of the spikes of *Lilaea* from hermaphrodite flowers. The evolution of the *Cyperaceae* advanced, however, further, and at least in the androecium there is a trend to trimery. The unstabilised conditions maintained themselves in the appearance of types with one, two, four stamens. In the *Cyperaceae* and *Gramineae* we therefore observe a similar evolutionary trend, only differently modifed. In both there is also a similar configuration of the styles, most often with two to three branches. This common character is very important for establishing the affinity of the two groups. The number of styles or stigmata is often given in relation to the number of carpels, of which the gynoecium was formed. But this applies to gynoecia really connate, and their connation shows also in the number of placentas. In the monocarpic types there is, however, often a division of the style into two to three branches. In this way it became fixed also in the styles of these two families. In the family *Cyperaceae* there is still a correlation between the number of stigmata and the shape of the fruits. The types with two stigmata have a lenticular fruit, those with three a trigonal fruit. This character is, however, of no great phylogenetic importance "since intergradations between them were observed, and also that the degree of difference varied with external growth factors" (Lawrence). They behave therefore similarly in some representatives of the group *Helobiae*. Thus they are not of so great a phylogenetic importance as in the *Liliaceae*, where they indicate mostly ancient conditions.

The varying conditions of the flower in the *Cyperaceae* indicate an origin in the euryplastic phase. Evolution advanced here rather far, almost to trimerous, pentacyclic flowers. There occurs here even the beginning of the formation of a flower with a somewhat coloured perianth. The whole family disintegrated into a great number of genera and species, which have a great, cosmopolitan distribution. The genus *Carex*, as the simplest type according to the preceding discussions, has also a correspondingly vast distribution and a great number of species. The great evolutionary vigour, which manifested itself in this genus, indicates an origin in the early euryplastic phase and a rich differentiation in the stenoplastic phase.

Restionaceae.

Herbs of grass-like aspect. Leaves linear, almost distichous, ligulate. Flowers in spikes, hermaphrodite or unisexual, tri- or monomerous. Perianth in two series, but often some segment is lacking, and sometimes there are also flowers without perianth. Stamens three or two, 1- to 2-celled. Ovaries superior, 1- or 3-celled, and stigmata 1 to 3. In each cell there is only one ovule. Mealy endosperm.

Very remarkable family, as it shows a similar evolutionary trend as the *Juncaceae* and *Cyperaceae*. Evolutionarily it is therefore a group on the transition between these two families. It shows, however, closer relations to the family *Juncaceae*, as most of the types have developed a tricarpellate ovary changing into a capsule. All basic flower parts vary in number in the *Restionaceae*. Perianth usually not developed, or trimerous, hexamerous, sometimes irregular as some segments are lacking. Therefore there are here developed all transitions from flowers without perianth to trimerous flowers with two series of the perianth. The flowers are most often dioecious, rarely monoecious, or hermaphrodite. The stamens vary less and are usually in one series of three, rarely two. The anthers are 1-celled to 2-celled. We find great variations also in the ovaries. There are here transitions from a 1-celled, tricarpellate ovary with connate styles via 3-celled ones with three imperfectly connate styles to a monocarpellate ovary with one to two stigmas.

A constant character is the general, grass-like habit and the membranaceous perianth. Below the flowers sterile bracts are usually developed, corresponding to the glumes of the grasses. The *Restionaceae* belong therefore with all characters into the graminoid evolutionary group. Evolutionarily they thus advanced far further than the *Cyperaceae* and *Gramineae*, and in many characters they approach already the *Juncaceae*.

A strange character appears in this family, which we observe, however, scattered also in different other evolutionary groups. It consists in the strikingly dimorphous inflorescences differing according to sex. The female inflorescences are like an unramified, dense, bractic spike with strikingly enlarged scarious bracts at the base. They resemble somewhat the inflorescence of the genera *Xyris* or *Schoenus*. The male inflorescences are ramified panicles of smaller spikelets, reminiscent of the panicles of the genus *Bromus* or of some species of *Carex,* or also *Juncus*. This character is very striking, and it seems that it is also very ancient, as we observe it also in the Gymnosperms.

Also the total habit, especially of the vegetative organs, varies much in this group. Some types are reminiscent of the genus *Ephedra,* others of the *Cyperaceae,* rarely they also resemble the genus *Typha (Anarthria).* The types forming clusters of twigs or leaves imitating a sterilised inflorescence are also interesting (e. g. in *Restio tetragonus,* etc.). This character may be phylogenetically important for an understanding of the relations between the inflorescence and the leaves. The whole organ looks like a sterilised inflorescence in which only the bracts are developed in the form of acicular leaves or green ramified axes growing in the axile of the bracts. Sheathing bracts are frequent, developed instead of leaves, and there is not yet in them any transformation into normal leaves. The *Restionaceae* are distributed mostly in the southern hemisphere, and the problems set by them cannot be solved satisfactorily from the herbarium material; a more detailed study in living plants would be necessary. It is possible that this group, otherwise evolutionarily considerably advanced, has preserved very primitive features in the shapes and functions of the bracts, leaves and axes, features which are important for an understanding of the relations between these organs. The great variability also of the other organs indicates that it is a very important group, which originated in the euryplastic phase, in which characters developed connecting the monocarpellate *Cyperaceae* and *Gramineae* with the tricarpellate *Juncaceae.* This does not mean of course that it is possible to derive them directly from this group, as these characters are only convergent. They help us to form an idea of the evolution, but they themselves are certainly not the parent types. Their evolution proceeded perhaps in a similar way, but in other types which probably did not preserve their plasticity. They developed further than the *Restionaceae,* which thus represent only a lateral evolutionary group.

Centrolepidaceae.

Small family of grass-like or moss-like aspect. Flowers small, hermaphrodite or unisexual. Sometimes subtended by 1—3 hairy bracts. They are arranged in heads, spikes, or rarely solitary ,and subtended by one to three glumelike bracts. Perianth absent. Stamen one, rarely two. Anthers one- to two-celled, versatile. Ovaries superior, of one to many carpels, growing on a stalked carpophore. Styles at the end of the carpels free or at the base more or less connate. Each carpel with only one ovule.

Phylogenetically this family is very remarkable, for some characters became fixed in it which we do not find in the other Monocotyledons.

Flowers without perianth, subtended by bracts, versatile anthers, and gynoecium with unstabilised number of carpels indicate that there was here a similar evolution as in the *Gramineae,* but that it was far more complicated as far as the evolution of the gynoecium is concerned. Though monocarpellate ovaries formed here, yet they are on the other hand almost apocarpous to syncarpous, connected mostly only by the central carpophore. On the whole this family was rather little evaluated phylogenetically. It shows some characters which vary considerably within the one family, from the simplest to the most complicated features. Especially the structure of the gynoecium is very remarkable and indicates a great evolutionary vigour at the time when these types were formed. Morphologically this family stands between the families *Restionaceae* and *Juncaceae* on the one hand and the *Cyperaceae* and *Gramineae* on the other hand. It shows how in the evolution in the euryplastic phase types with very different structures arose, which could give rise to quite different evolutionary groups.

Thurniaceae.

The family *Thurniaceae* comprises only the genus *Thurnia.* On the whole it belongs by its structure in the affinity of the *Juncaceae.* It differs by the inflorescence, which is rather remarkable. The perianth has an irregular arrangement, and the flowers are placed in dense heads, subtended by green bracts. They are reminiscent of some *Cyperaceae.* The trimerous, pentacyclic flowers indicate a similar evolutionary position as that of the *Juncaceae.* They differ from the latter only by the irregular arrangement of the perianth segments, and this betrays the somewhat unstabilised evolutionary conditions under which this family was formed.

Flagellariaceae.

Tall herbs, often climbing, with parallel veined, sheathing leaves. Flowers small, in panicles, hermaphrodite or dioecious. Perianth in two trimerous series, small or somewhat coloured. Stamens 6. Ovary superior, of three carpels, 3-celled, with one ovule in each cell. Style three-branched. Fruit indehiscent, dry, or fleshy, seeds with mealy endosperm.

Phylogenetically somewhat unclear family, which is often placed in the affinity of the *Liliaceae* or *Commelinaceae.* It belongs to the trimerous, pentacyclic types, whose affinity is sometimes difficult to ascertain. They are the result of a parallel evolution in almost all evolutionary groups. When no striking characters are developed in them, characteristic for a certain group, their affinity is not clear. It is not excluded that evolutionarily different groups may have been combined in the trimerous and pentacyclic groups. In these groups a different evolution is indicated only by the characters of the vegetative organs and sometimes also by anatomical details. In the family *Flagellariaceae* the inconspicuous perianth, the undifferentiated calyx and corolla, rarely somewhat petaloid, agree with the evolution of the graminoid group. The leaves agree also with this, but there was here a far greater complexity owing to the formation of tendrils. These appear, however, in several places in the *Liliaceae,* e. g. in *Fritillaria ruthenica, F. verticillata, Gloriosa,* and many dicotylophyll groups. Thus this organ is nothing very rare and arose independently in different evolutionary groups. The shape of the pollen speaks also for an inclusion in the affinity of the *Gramineae.* For these reasons it is possible to assume that the *Flagellariaceae* belong to the graminoid evolutionary group. In the structure of the flower they are, however, a somewhat extremely configurated type standing on a similar level as the *Juncaceae* with a more stabilised evolutionary vigour.

Juncaceae.

Plants of grass-like aspect. Leaves linear, often reduced to sheaths only. Flowers inconspicuous, hermaphrodite or dioecious, with perianth in two, more rarely in one trimerous series. It is rarely somewhat coloured. Stamens 6 in two series, rarely 3 in one series. Gynoecium superior, tricarpellate, 1-celled or 3-celled. Ovules one to many in each carpel. Styles one to three, but always 3 stigmata. Fruit a capsule.

The *Juncaceae* are most often placed in the affinity of the family *Liliaceae.* The whole trend of the evolution is, however, in this family different, and only the common structure of the flower could connect them. This structure of the flower is, however, very probably due to convergent evolution, i. e. to the similar material predisposition of all Monocotyledons. The other graminoid families are evolutionarily far nearer. When we start from the pentacyclic, trimerous types as basic types, it would be easy to connect all terminal types of the different evolutionary groups, of the *Juncaceae, Bromeliaceae, Liliaceae,* etc. Thus an apparently homogeneous group is formed with a similar structure of the flower. But the other groups could be derived from this group only by reduction. Further the initial group would be very stable and highly defined, and the so-called derivate types would be very variable. A strong evolutionary vigour must manifest itself in great changes of the basic organs, and often in the origin of lateral groups, in which these variable conditions may have become stabilised, whereas the terminal members of evolution will preserve invariable conditions in the basic organs. Though under meso-evolutionary conditions many modifications of the shapes may arise, these will already preserve the basic structure and change mostly only quantitatively. The result of this will be many different genera, but on the whole of a uniform structure. Progress from simple to more complicated shapes and properties explains, however, far better the processes which probably governed evolution than mere reduction.

The *Juncaceae* are a family fairly stabilised in its basic structure. Thus it seems more probable that we have here a family in which the predispositional properties asserted themselves completely. Thus they represent the end of an evolutionary line leading from simpler forms to more complicated forms. This does not mean of course that they must have originated gradually over a long period. Their origin may on the contrary have been almost contemporaneous, and the difference may lie only in the rate of the stabilisation of the evolutionary vigour.

The monotypical genus *Prionium serratum* had an evolution somewhat different from that of the basic types of the family, and one which led to the formation of a different habit. It resembles some species of the family *Xanthorrhoeaceae.*

Summary: The graminoid evolutionary group comprises a number of families characterised by similar evolutionary trends, and which probably differentiated from a common stock. They have an inconspicuous perianth, not differentiated into calyx and corolla, and grass-like leaves often reduced only to bracts. Most of the families are most often derived from the *Liliaceae* by reduction. This derivation does not seem justified, as the *Liliaceae* are an evolutionarily too stabilised family which represents rather a predisposed terminal type of the Monocotyledons than an initial group. It is far more probable that the evolution of the graminoid group started from simpler types which became gradually more complicated. It is possible to assume that the types differentiating themselves earlier will show a greater variability in the configuration of the different characters than the more stabilised types. It is of course possible that the terminal groups, predisposed by the material foundation, will differ rather in the general habit than in the structure of the flower, to which the evolution of all groups tended. Thus such a group would include types with a similar structure of the flower, but of different origin. The correct solution of the problem of such convergent evolution is possible only step by step and is one of the most difficult taxonomic problems. Thus in the graminoid type there occur in different families densely leafed types differing considerably from the other types. In the *Juncaceae* these are the genera *Andesia, Oxychloe* and *Distichia,* in the *Centrolepidaceae* the genera *Gaimardia, Alepyrum,* and in the *Cyperaceae* the genus *Oreobolus*. One might raise the question whether these types represent a separate group or are only certain predisposed modifications accounting for the homologous variability of the individual families. The solution of this problem will be possible only after the detailed analysis of the characters and properties of all the relevant types. Also the sepaloid evolutionary group is distinguished by similar twofold, moss-like and grass-like, types. It is possible that just this character indicates a close relationship of the two groups.

In the graminoid evolutionary group an evolution from simple apocarpous types to syncarpous tricarpellate types is probable. This conception is strengthened also by the fact that in the apocarpous or monocarpous types we often find a very considerable variability in the configuration of the flower parts. In the syncarpous types, on the contrary, there is a relatively considerable stability of the structure of the whole flower. Already from this it is possible to infer that the splitting off of the first types took place in a different evolutionary phase than in that of the second types. Their manifold structures indicate an origin in the euryplastic phase in the unstable types and a later differentiation in the stable types. The stabilisation of the morphologically homogeneous types indicates that evolution advanced as far as the most stable predisposed forms.

The differentiation of the graminoid evolutionary group proceeds already in a certain direction. It is possible to align the families from monocarpous via apocarpous to syncarpous types. Each phase is represented by a few families. The monocarpous and apocarpous link up with the hydrophile group, of which the families *Lilaeaceae, Juncaginaceae* and *Scheuchzeriaceae* are directed towards the graminoid group or may even belong to it. The families *Restionaceae* and *Centrolepidaceae* represent two families in which we observe a similar evolutionary trend as in the whole group. There are here monocarpous, apocarpous to syncarpous types. The families *Juncaceae, Thurniaceae* and *Flagellariaceae* represent the terminal, most complicated and evolutionarily stabilised type characterised by trimerous, pentacyclic flowers with syncarpous ovaries. It is only the families *Centrolepidaceae* and *Restionaceae* which have a development of different evolutionary phases within one family. Thus the isolation of the individual phases within these families gives us a conception of the evolution of the whole group.

The Xeranthemous Evolutionary Group.

To the xeranthemous evolutionary group belong families with a characteristic structure of the inflorescence. The flowers are most often arranged into dense heads, or spikes, and have always bracts at the base. The perianth is mostly scarious. Outer and inner series of the perianth are differently configurated, but not developed as typical calyx and corolla. They are very closely related to the graminoid group. They are distributed chiefly in the southern hemisphere.

Eriocaulaceae.

Herbs with linear, grass-like leaves, sometimes only membranaceous, growing mostly in swamps. Flowers arranged in heads, with an involucre of bracts at the base, which are reminiscent of the inflorescence of the *Compositae.* Flowers actinomorphic or zygomorphic, small, monoecious or dioecious. In the monoecious flowers both sexes are mixed or the males are in the centre and the females around them. The perianth is scarious, in two series, but does not form a green calyx and coloured corolla, though these are usually different in shape. The outer series is usually of two to three segments, free or somewhat connate; in the inner series they are infundibular cupular connate, rarely absent. Stamens 4—6 in two series, rarely only two or three. Ovary superior, 2- to 3-celled. In each cell one orthotropous ovule. Style one, with two to three branches, often subdivided. Fruit a 2- to 3-celled capsule. Endosperm abundant.

Phylogenetically an interesting family with some characters occurring only rarely in the other Monocotyledons. The most characteristic feature is the flower head. Evolutionarily similar principles show here as in the *Compositae,* of course in an entirely different evolutionary group. Notwithstanding its great homogeneity and extremely formed inflorescence this family shows a considerable instability in some other basic characters. The habit differs greatly. There occur here types forming rosettes at the base of linear leaves from which grow scapes terminated by heads, further densely leafed stems with axillary umbels on long scapes, and short leafed stems with axillary, short-stalked heads. The flowers are trimerous or dimerous, and sometimes both in one genus. In some species the trimery changes into dimery in the flower. Thus the trimerous flowers of *Philodoce cuyabensis* have only two stamens and *Lachnocaulon digynum* has only two carpels. Often some series are absent or are differently configurated. Thus with the sex dimorphism of the flowers a very different formation of the perianth is connected. In the female flowers it is sometimes even lacking or there is only the inner series. The outer and the inner perianth often change according to the sex. In the male flowers the outer perianth is often connate infundibular, sometimes also rudimentary. In the female flowers two segments are sometimes keeled and the third is of different size, either larger or smaller. Also the inner perianth is often connate cup-shaped in the female flowers, and only rarely free. In other cases it is rudimentary or absent, or the segments are of different sizes. These conditions show that the *Eriocaulaceae* originated in the euryplastic phase as a lateral group, which in the stenoplastic phase strongly differentiated into many species. Here belong 12 genera, but more than 1100 species. They are distributed throughout the world and have sometimes rather disjunctive areas. The different structure of outer and inner perianth, the unequal configuration of the individual sepals, the appendages on the styles, the bractlike sheaths on the scapes, the crowding of the flowers into inflorescences, etc. indicate an affinity to the xerathemous group.

Xyridaceae.

Bunchy herbs with linear sheathing leaves at the base, growing mostly in swamps and in water. Terminal inflorescence in heads or spikes with sterile bracts at the base. Flowers hermaphrodite, moderately zygomorphic, with bracts. Calyx trimerous, rarely dimerous, with lateral segments boat-shaped and the inferior ones hood-forming above the corolla. Corolla tubular, actinomorphic, tri-lobed. Stamens three and often also three staminodes with moniliform hairs. Ovary superior, 1-celled or almost 3-celled. Style one, stigmata one to three. Ovules not many to numerous, rarely only one. Capsule enveloped by corolla tube. Seeds with mealy endosperm.

Small family from the affinity of the *Eriocaulaceae*. The evolution of the flowers has reached a rather considerable perfection, but also some irregularities stabilised themselves. Thus this family stands a little apart from the others. It arose probably at the end of the euryplastic phase when the evolutionary vigour had already stabilised itself. The zygomorphic flowers and irregularly configurated calyx, the appendages of the style *(Abolboda)*, the plumose and often bifid staminodes, and especially the habit characterise this family. By the general habit, the inflorescence and the structure of the flowers it belongs to the xeranthemous group. The centre of this family lies in tropical to subtropical America. Only few species grow in Africa, tropical Asia and a few more in Austraia. Thus they have a similar evolutionary centre as the Angiosperms, and this may indicate a great age of this family.

Rapateoceae.

Herbs with parallel veined leaves, rarely petiolate. Flowers hermaphrodite, actinomorphic. They grow in heads at the end of the scapes in axiles of one or two bracts or without them. The individual flowers carry on the pedicel numerous imbricately overlapping bracts. Calyx hyaline, trimerous, often connate at the base in a tube. Corolla trimerous, rarely free. Stamens 6, mostly by two behind each petal. Anthers at the base 4-celled, above 1-celled. Ovary superior, 3-carpellate, 3-celled. Style and stigma one. Ovules one or several in the cell. Fruit a capsule. Seed with mealy endosperms.

Small family distributed in tropical South America and West Africa. The structure of the flower is perfect and fairly stabilised. By the inflorescence and structure of the flowers it differs from the other families. Sometimes there is a rudimentation of two carpels and only one, apparently monocarpic carpel develops. The whole evolutionary trend is similar to that in the xeranthemous group and somewhat even to that in the graminoid group. Very probably it belongs to the affinity of the xeranthemous group as a lateral evolutionary line. By the structure of the inflorescence it is similar to that in the Gramineae.

Xanthorrhoeaceae.

Mostly xerophytic plants, sometimes with a woody stem. Leaves linear, either long in a basal rosette or short acicular, densely arranged on the stems. Flowers hermaphrodite or dioecious, solitary or some together, often also small and densely crowded into spikes or heads. At the base of the flowers are usually sterile bracts. Perianth of 6 segments in two series, most often membranaceous; sometimes coloured. Stamens 6 in two series, rarely three *(Johnsonia).* The inner series cohering to the base of the outer perianth. Ovary superior, 1- or 3-celled, three-carpellate. Fruit a capsule with many seeds or rarely a nut with one seed enveloped in a persistent perianth.

The family is most often placed in the *Liliaceae* on the basis of the same structure of the flower. Hutchinson correctly separated some types as an independent family, but its definition seems to be too narrow. We observe a similar evolutionary trend also in some tribes which he left among the *Liliaceae*. Thus the monotypical *Aphyllanthideae,* and also the *Johnsonieae* agree well with the *Xanthorrhoeaceae.* These types have all been wrongly placed within the Monocotyledons. They are placed in the affinity of the *Liliaceae* or are connected with the *Agavaceae.* Both these families belong to the tepaloid group. The *Xanthorrhoeaceae* have, however, evolutionarily not much in common with this group. They belong clearly to the affinity of the family *Eriocaulaceae* of the xeranthemous group. They have not only a similar structure of the flower as this family but also many other characters which are extreme in the Monocotyledons, such as the dry perianth, the tendency to form dense inflorescences, the sterile bracts at the base of the inflorescence or solitary flowers, the tendency to dioecie, etc. This shows most strikingly in the homologous variability of the two groups. Both groups include some rather deviating types, the most frequent of which is a type with long, basal, grass-like leaves and leafless scapes terminated mostly by a dense inflorescence. Another type has narrowly linear leaves placed densely on the stems, and from them grow short-stalked scapes with bracts with flower heads. The individual genera comprise usually only one of these types, but sometimes both types are found in one genus *(Laxmannia)*. This remarkable homologous variability is the best proof of the relationship. It is unimaginable that such a phenomenon could occur fully agreeing in two remote evolutionary lines. A convergent evolution due to material predisposition never leads to such remarkable agreements, especially when these do not represent an advantageous response of a general predispositional evolutionary trend to outer conditions. The evolutionary trend extends usually only to the rough structure of the flower or the habit, but mostly not to the details. Agreeing details betray always a close relationship. In the *Eriocaulaceae* and *Xanthorrhoeaceae* there occur, however, also other striking agreements, as the membranaceous perianth, the bracts at the base of the inflorescence, the dense heads, etc.

Both families show striking differences in the aspect of the individual types. To the *Xanthorrhoeaceae* belong the *Aphyllantheae, Johnsonieae, Dasypogoneae, Lomandreae,* and *Calectasieae*. All show a similar evolutionary trend, entirely different from that of the *Liliaceae* and agreeing with that of the *Eriocaulaceae*. Some genera have also some peculiarities in common; thus *Calectasia* and *Borya* agree in having articulated leaves. Certainly the differences of the individual tribes are not so great that they would have to be separated into different families.

Summary: The xeranthemous evolutionary group comprises families which were placed in two remote evolutionary groups. They show, however, very striking agreements in the structure of the flower and in general aspect. The following families belong to this group: *Eriocaulaceae, Xyridaceae, Xanthorrhoeaceae,* and *Rapateaceae*. They are families mostly tropical, richly developed mainly in the southern hemisphere. It is a very small and evolutionarily considerably homogeneous group. It is very close to the graminoid group and especially to the family *Juncaceae*. It agrees with this family also by the structure of the flower as well as by general aspect. It is not excluded that w have here a group which might be united into a common group with the graminoid group. It differs, however, by some characters and therefore it was separated as an independent group. It has also close relations to the sepaloid group (moniliform leaves, style with appendages, etc.).

Sepaloid Evolutionary Group.

This group includes families with perianth differentiated into calyx and corolla, characteristic bracts under the inflorescence. A trend can here be observed to various modifications in the androecium and to the formation of symmetrical or even asymmetrical flowers. Gynoecium always syncarpic, tricarpellate.

Commelinaceae.

Herbs sometimes pulpy, with a rosette of basal leaves, or noded leafed stem. Rarely occur also climbing types. Leaves parallel veined, sheathing. Flowers actinomorphic, rarely zygomorphic, hermaphrodite, aranged in clusters, panicles, or solitary. Often they have at the base bracts, spathelike or green. Perianth differentiated into trimerous calyx and corolla. Rarely the calyx is somewhat petaloid. Petals sometimes connate into a tube, sometimes one segment is far smaller. Stamens 6, but sometimes three as staminodes, rarely 5 staminoles *(Callisia)*. Filaments of the stamens mostly with moniliferous hairs. Ovary superior, sometimes stalked, 3-celled, rarely 2-celled *(Floscopa)*. Several ovules in each cell. Style one, stigma capitate or trifid. Fruit a capsule or fleshy, indegiscent. Seeds with mealy endosperm.

A phylogenetically remarkable family. On the whole it is possible to observe in it a trend to the formation of trimerous, pentacyclic flowers with a remarkable differentiation of calyx and corolla. Mostly, however, the structure of the flowers exhibits various irregularities. There is here a tendency to form zygomorphic flowers. Sometimes all the petals are not equal; but especially in the stamens we find a frequent differentiation into several types according to their position in the flower. Sometimes the whole series or also individual stamens are developed as staminodes. It is only rarely, in some genera, that all the stamens are equal. More often they are different either according to the series or irregularly. There is an abundance of variously enlarged connectives, various appendages on the filaments, hairy or bald filaments, etc. The genus *Cochliostema* shows somewhat similar conditions as the family *Orchidaceae*. Here only one posterior fertile stamen is developed of the outer series, and two lateral stamens with coloured appendages enclosing the anthers are developed of the inner series. The other stamens are only developed as staminodes. Also the ovary is mostly 3-celled, at most 2-celled. A carpophore is rarely developed. In some genera two cells are rudimentary and an apparently monocarpellate fruit develops *(Rhoeo)*.

On the whole its evolution is thus directed towards the formation of a trimerous and pentacyclic flower, but it reaches this goal only rarely. Often it is crippled and shows a tendency to the formation of unequal members in the individual series.

The *Commeliaceae* originated probably in the euryplastic phase, but they show a relative stabilisation of the basic structure.

Mayacaceae.

Small monogeneric family of aquatic plants with dense leaves, narrowly linear, bidentate at the end. They resemble the mosses. Flowers hermaphrodite, actinomorphic, axillary, solitary, or several together, with membranaceous bracts at the base. Perianth differentiated into trimerous calyx and corolla. Stamens 3 with 4-celled anthers. Ovary superior, one-celled, tricarpellate; style and stigma one. Fruit a capsule. Seeds with endosperm, capped by a small stopper.

Phylogenetically this family is somewhat extreme, notwithstanding the generally stabilised structure of the flower. It exhibits, however, some peculiarities such as the development of only one series of stamens, 4-celled anthers, leaves bidentate at the end, seeds capped by a small stopper, etc. Thus it is not possible to join it to some other, larger family. Notwithstanding the more complicated structure of the flower there occur in it some characters which we observe in simple families. Thus its ecology is similar to that of the *Helobiae*, its aspect and differentiated perianth make it resemble some genera of the family *Hydrocharitaceae*, it has 4-celled anthers like *Najas*, a stopper on the seed like *Lemna*, bracts at the base of the flower pedicels like many *Helobiae*. Nevertheless it shows the closest affinity to the family *Commelinaceae*, with which it agrees by the structure of the flowers, the shape of the pollen, the ornamentation of the seeds, etc. Nevertheless it stands somewhat apart from this family, and because of the modifications mentioned above it approaches also the group *Helobiae*.

Musaceae.

Large herbs or trees. Leaves huge, with thick midrib and numerous pinnately parallel nerves. Flowers in spikes or panicles, subtended by spatheceous bracts, uni- or bisexual. The perianth is composed of 6 unequal segments in two series, free or variously connate. Except for *Orchidantha* they have a perianth undifferentiated into calyx and corolla. Stamens, by threes, in two series, of which one is usually a staminodium, sometimes coloured; only *Ravenala* has all fertile. Ovary inferior, 3-celled, with many ovules, rarely with only one *(Heliconia)*. Style one, stigmata three and often lobed. Fruit an elongated berry or a capsule. Seeds with endosperm.

This family represents one of the extreme types of the sepaloid evolutionary group. It shows a tendency to form irregularities in the flowers. In consequence of this tendency it can easily come also in related types to far more essential changes than in types with actinomorphic flowers. Some authors raise the individual types to independent families because of the great morphological differences in the structure of the flowers. The irregularities bring with them a certain structural lability leading to the formation of considerable modification. The vegetative organs are, however, uniform and do not form any irregularities.

The *Musaceae* show that their differentiation took place in the euryplastic phase. They as well as the other *Scitamineae* are rather different from the remaining groups. Thus their placement varies. Often they are referred to the affinity of the *Orchidaceae,* which have a similar evolution in the irregularities of the flower. The evolutionary trend is in both families rather similar, but the changing characters are different. We have here much more probably a convergent evolution of parallel evolutionary groups than true affinity. They show a far closer affinity to the *Bromeliaceae.* Though in these it came to the development of actinomorphic and perfect flowers, yet there appear in them a whole number of common characters. In both there is a tendency to the formation of symmetrical flowers, petaloid sepals, coloured bracts, similar fruits, similar inflorescences with bracts, cohering members of the same series, fairly similar shapes of the pollen, etc. But they differ in the structure of the leaves, the non-development of certain flower parts, and especially by modifications in the androecium. Notwithstanding the on the whole great differences of the two groups it seems that the *Bromeliaceae* and the *Scitamineae* have a sufficient number of characters in common and that they belong very probably to a common evolutionary group.

Zingiberaceae.

Herbs with tuberous rhizomes. Leaves large, pinnately veined, sheathing, distichous, ligulate. Flowers solitary, in spikes or racemes, subtended by conspicuous bracts. They are usually hermaphrodite, symmetrical and asymmetrical. Perianth 6-merous in two series. Calyx green, connate, corolla tubular, with the posterior segment largest. Fertile stamens one, and one large petaloid one as staminode. Rarely two more staminodes are developed from the outer series. Ovary inferior, 3-carpellate, rarely 2-carpellate, 3-celled or 1-celled, rarely 2-celled. Style one, rarely two, enveloped in a groove of filament of the fertile stamen. Fruit a capsule or berry.

The *Zingiberaceae* form together with the other *Scitamineae* a homogeneous group characterised by its crippled flowers and pinnately veined leaves. In all these families the individual representatives differ in the basic organs, and often rather essentially so. Nevertheless the evolutionary trend of all the modifications is fairly similar. Thus there are great differences in the development or abortation of the individual stamens in the androecium. A strong variability is, however, common to all. The family differentiated into 47 genera, most of which have, however, a small distribution, and only two, *Costus* and *Renealmia,* have large areas. The great variability of the characters in the individual genera and the pantropic areas indicate an origin in the euryplastic phase.

Cannaceae.

Closely related and similar family, distinguished by the leaves without ligule and the free calyx. Stamens of the outer series sterile, petaloid, cohering basally, in the inner series two petaloid, sterile, in a labellum, and one divided, one half with a 1-celled anther, the other half coloured. Ovules many, and in this distinguished from the following family. The family represents only the most extreme type of the *Zingiberaceae* and has only one genus, *Canna.*

Marataceae.

Closely related and similar to the preceding family. The distinguishing feature consists in the asymmetric leaves, which are noded between the blade and the petiole. Calyx free, corolla connate at the base, irregularly 3-lobed above. Fertile stamen one, as in the *Cannaceae*. The other two stamina petaloid, and one of them hooded and covering in youth the centre of the flower. The outer series of stamens form one or two petaloid staminodes. Ovary inferior, 3-celled, often two cells sterile. In each cell one ovule. Fruit a capsule, berry or achene. The seeds have perismerm and endosperm.

The family is often regarded as the most advanced of the group *Scitamineae* owing to the very irregular development of the androecium restricted to only one stamen and to the gynoecium containing only one egg. It seems, however, that from an evolutionary point of view it is not possible to regard this complication as progressive. They represent only a lateral group in which unusual modifications stabilised themselves, but these did not attain the perfection of predisposed types.

Bromeliaceae.

Herbs, rarely epiphytic, more rarely terrestrial, woody plants. Leaves in a basal rosette, rarely also cauline, mostly parallel veined, rarely pinnately veined *(Pitcairnia)*. Inflorescence terminal in racemes, panicles, rarely solitary. Flowers hermaphrodite, rarely polygamous or dioecious, actinomorphic, rarely symmetrical. Perianth differentiated, cohering or free. It is only rarely that the calyx is coloured *(Sodiroa)*. At the base of the petal often scales like the squamulae intravaginales on the leaves of the *Helobiae*. Stamens 6 in two series. Ovary 3-celled, connate of three carpels, inferior or superior, rarely semi-inferior. Style one, stigmas usually three. Fruit in superior ovaries mostly a capsule, in inferior ones a berry. Seeds numerous, with abundant mealy endosperm.

Phylogenetically this family represents a group which is very stabilised according to the structure of its flower and general aspect. It preserves always a trimerous, pentacyclic and syncarpous flower. In the details there are here often great differences in the formation of the vegetative as well as of the sexual organs. This variation can sometimes be observed also in individual genera. Thus e. g. in the genus *Pitcairnia* there are herbaceous to woody types, linear to petiolate broad leaves, calyx and corolla free to connate, flowers actinomorphic to symmetrical, ovaries superior, semi-inferior to inferior, berries and capsules, caducous and non-caducous leaves, heterophyly, terrestrial and epiphytic types, etc. It is the most variable genus of the family. Somewhat less variable is the woody genus *Puya*. In this genus some types resemble the genus *Agave* and have a trunk up to 10 m. high. Often there are here also types which die after having flowered. Some have tuberous rhizomes. Only few types developed other characters than those which we observe in the genus *Pitcairnia*. Thus the genus *Hechtia* has dioecious flowers, *Navia* anemophilous flowers, *Sodiroa* a coloured calyx. On the whole we find here only a slightly smaller variability than in the families *Liliaceae* and *Amaryllidaceae*. Evolutionarily they show an affinity to the family *Commelinaceae* and also to the *Scitamineae*. The wealth of types indicates an ancient origin of the families. They have a stabilised type of the flowers and a lesser area, restricted mostly to tropical America. Only one species in West Africa *(Pitcairnia feliciana)*.

The importance of an inferior or superior ovary for the affinity is in this family rather clearly visible. It does not seem as if this character could play a great rôle in the distinction of the types, and it can vary also within one genus. Thus it has always to be evaluated carefully in order not to overestimate it. Hutchinson seems to have used this criterion correctly in valuating the *Liliaceae* and *Amaryllidaceae*.

Summary: The sepaloid group comprises families characterised in most members by a perfectly differentiated perianth into calyx and corolla. But this character is by no means quite uniform, and we find sometimes also types with a coloured calyx *(Musaceae, Zingiberaceae, Commelinaceae, Bromeliaceae)*. This is, however, rather the exception than the rule, and heterochlamydic types belong always to the close affinity. An interesting feature of the group is that it does not show any evolutionary trend from apocarpous to syncarpous types. The carpels have preserved only rarely complete independence. Thus in some *Marantaceae*, in *Rhaeo*, only one carpel is as a rule developed, and thus there may be an apparent monocarpy. Also in the *Bromeliaceae (Hechtia* and *Puya*) there is no complete coherence of the carpels, and these maintain a certain independence. The whole group is predominantly syncarpous. Perfectly trimerous, pentacyclic flowers have but little differentiated here; we find them only in the *Bromeliaceae*. Part of the families preserves the basic structure of the flower, but especially the androecium is subjected to considerable variations in the *Scitamineae, Commelinaceae* and *Mayacaceae*. The variations in the formation of the androecium constitute a very characteristic evolutionary character of this group. There are relatively few variations in the gynoecium, which is mostly tricarpellate, and we find but rarely, in the *Commelinaceae* and *Zingiberaceae,* dicarpellate ovaries. The leaves preserve mostly a grass-like shape with parallel veins, and broad leaves are rare. The broad, pinnately veined leaves of the *Scitaminae* are characterised by somewhat modified shapes; but as we can tell from some other families, this is not a deviating evolutionary character; in the grasses too we can find types which pass into pinnately veined leaves *(Pharus)*.

A characteristic feature of this group is the independence of the sepals and petals. Very often they are formed in a deviating and independent way. Except for the *Bromeliaceae* there are here predominantly types adapted to damp habitats. In the others there are mostly arrangements for catching rain water in the leaf sheaths. They have as a common feature also the bracts under the inflorescence, often strikingly green or coloured. The trend to form symmetrical and asymmetrical flowers is fairly marked. Woody types are also rare. The group shows a closer relationship to the graminoid and xeranthemous groups, and a more remote one to the hydrophile group.

The Dicotylophyll Evolutionary Group.

This group comprises families in which there is a considerable inclination to form dicotyle leaves, but also parallel nerved leaves are not rare. Climbing types are also frequent; they are woody, with flowers in apparent umbels, with tuberous rhizomes, etc. The flowers have often an undifferentiated perianth, and more rarely there is a different development of the outer and inner series of the perianth.

Trilliaceae.

Herbs with thick or creeping rhizomes. Stems simple at the base with several leaf-sheaths. Leaves broad, reticulately veined, opposite or in whorls. Flowers terminal, solitary or several in umbels, hermaphrodite, actinomorphic. Perianth segments free, sometimes the outer ones greenish, the inner ones coloured, sometimes almost undifferentiated. They are 4- to 6-merous, rarely up to 10-merous. Stamens 4—6, rarely 8—12. They usually have produced connectives. Sometimes, however, there occur within one genus produced and non-produced connectives *(Paris)*. Ovary superior, 1- to 3-celled, rarely 4- to 10-celled. Styles 3—5, free, or one with three to five branches, rarely 4 to 10. Ovules numerous. Fruit a capsule, rarely a berry.

The family is placed most often in the *Liliaceae*. But dicotyle leaves, produced connectives, variations of the flower parts are alien to this family. Therefore Hutchinson was fully justified in separating it as an independent family. The evolutionary trend which shows in it, agrees, however, with that shown by the dicotylophyll group and especially by the family *Roxburghiaceae*. In both families we find variations in the number of the flower parts, opposite leaves, 1-celled ovaries, creeping rhizomes, dicotyle leaves, a somewhat differentiated perianth, produced and non-produced connectives, superior ovaries, solitary flowers or umbels with several flowers, etc. Thus evolutionary characters show themselves in it which we observe, except for pentamerous flowers, also in different families of the dicotyplophyll group. The variations in the number of flower parts are very great, and evolutionarily remarkable. Though we find here trimerous flowers *(Medeola, Scoliopus, Trillium)*, yet in the genus *Paris* they vary entirely irregularly between 4- and 10-dimerous. There occur also pentamerous flowers, exceptional in the Monocotyledons; but they occur here on the whole as an irregularity. These facts indicate that the family originated very early, and that also some indefinite conditions became stabilised in it. This shows the great age of the family. Against this would speak the small areas of the family; but we have mostly mountain species, and thus it is possible that they had no opportunity to spread across the tropical region. The spreading was obviously much later than the origin of the family.

Aspidistraceae.

Rhizome herbs with large, mostly petiolate leaves. Flowers actinomorphic, hermaphrodite, in dense bractic spikes, or also solitary on axillary scapes. Perianth 3- to 4-merous, campanulate, connate, with short lobes. Stamens 6 or 8, ovary 3- to 4-celled, with 2 to 6 ovules per cell. Fruit a capsule. Style broad, ending shield-shaped by connate stigma-lobes. This family comprises the genera *Rhodea, Campylandra, Tupistra* and *Aspidistra.* The genus *Gonioscypha* is evolutionarily different and belongs presumably to the *Liliaceae.* The sheathing leaves and shape of the stigmas of this genus are different. Most often this family is placed in the affinity of the *Liliaceae;* but the trend of evolution in the structure of the vegetative as well as of the generative organs is entirely different. We find, however, a very similar trend in the family *Taccaceae,* which is rather similar in the structure of the flower as well as of the vegetative organs. From an evolutionary point of view the *Aspidistraceae* have to be separated from the *Liliaceae,* as the former have obviously common ancestors with the *Taccaceae.* But even the *Polygonateae,* which are placed in the close affinity, are not directly related to this family, though they may have common ancestors.

Taccaceae.

Herbs with tuberous to creeping rhizomes. Leaves basal, petiolate, large, entire, rarely much lobed pinnately or pedate. Flowers actinomorphic, hermaphrodite, often in apparent umbels, at the base with conspicuous bracts, which are sometimes coloured. Prophyll thread-like. Perianth connate, 6-lobed, of a dark colour. Stamens 6, in the genus *Tacca* with scutate appendages. Ovary inferior, 1-celled, 3-carpellate. Style one. Stigmas three, 2-lobed, often leaf-like widened and umbrella-like reflexed over the style. Thus the stigmas are on the underside. Ovules numerous. Seeds with abundant endosperm. Fruit a berry or capsule.

This family is rather isolated among the Monocotyledons, and only the *Aspidistraceae* and *Trichopodaceae* have a similar configuration. It has been referred to very different affinities. Often it is said to be related to the *Aristolochiaceae.* More often, however, its relation to the *Hypoxidaceae* is pointed out. But also relations to the *Burmanniaceae* and *Orchidaceae* have been given. These families show, however, a different evolutionary trend, and are probably not related. Also the *Iridaceae* are regarded as related because of the stigmas, but this is the only common character, most probably convergent. The same evolutionary trend shows itself, however, in the *Aspidistraceae,* which are very closely related by the whole structure of the flower, the habit, and especially the shape of the stigma. It seems also rather closely related to the family *Dioscoreaceae.* Especially the genus *Trichopus* is not too remote either habitually or in the structure of the flower. The ribbed ovary, long pedicel, dicotyle leaves, produced connectives, etc. are characters common to both groups. They differ by the parietal placentations which occur, however, also in some other families of this group. Also divided leaves are frequent in the *Dioscoreaceae*. Thus it seems that the placing of the *Taccaceae* in the dicotylophyll group is not forced; and that it answers best the whole evolutionary trend of this family.

Ruscaceae.

Herbs with rhizomes, or woody plants, often climbing. Instead of leaves there are often phylloclades. Flowers hermaphrodite or dioecious. Pedicels often articulated, perianth free or connate. Stamens six or three, filaments free or connate. Ovary superior, 3- or 1-celled, most often with two ovules per cell. Fruit a berry or capsule.

The *Ruscaceae* are defined more narrowly or more widely. Sometimes they are referred as a subfamily to the *Liliaceae*. It seems, however, that it is necessary to connect in this family all closely related types of the family *Liliaceae* whose evolution has a similar trend as that of the *Dioscoreaceae*. They have also many other characters in common. Though there thus arises a somewhat wider family, this is homogeneous. The types alien to the *Liliaceae* are thus removed from among them. Also the genera *Herreria* and *Clara* have to be placed here. Their climbing stems, sometimes armed with prickles, tuberous rhizome, cluster of cladode-like leaves, articulated pedicels, winged seeds, etc., agree completely with the other types of the family *Ruscaceae* and with the trends of the whole evolutionary group. Similarly the genus *Asparagus* cannot be excluded from this family. The genus *Myrsiphyllum* with broad, cladode-like leaves agrees perfectily with the other members of the family and group. *Ruscus, Danae* and *Semele* are the prototypes of the families. To this family or in its close affinity belong, however, also most of the genera of the *Polygonateae* and perhaps also of the *Convallarieae*. The articulated pedicels, berries, large leaves, inflorescence frequently arranged in umbels, passing to solitary flowers, the sympodial structure of the stems, the thickened rhizomes, small number of ovules, etc., indicate a close affinity to the genus *Asparagus,* and with this the evolutionary trend of the dicotylophyll group. Only the agreement in the structure of the flower made it possible to refer it to the *Liliaceae*. The family thus defined, though rather wide, is not unnatural. It has a world-wide distribution, dividing into a number of isolated types. This is in keeping with the great age of the family. Also with these features it approaches the properties of the other families of this group.

Smilacaceae.

Group closely related to the family *Ruscaceae*. It is characterised by dioecious, rarely hermaphrodite flowers and 1-celled anthers. The sheaths of the leaves are often transformed into long tendrils. These characters as well as the dioscoreous leaves, the small number of ovules, berries, climbing, often prickly stems, umbellate inflorescence, woody character, thick rhizomes, etc., make it fit perfectly into the dicotylophyll evolutionary group, into the close affinity of the *Ruscaceae*. It is a very homogeneous group and was, just like the *Ruscaceae,* referred to the *Liliaceae*. But there are here variations in the number of the stamens. In *Pseudosmilax* there are 9—15 free stamens, and in *Heterosmilax* 3 connate in a tube. The world-wide distribution indicates a great age notwithstanding the small number of genera, and similarly the changes in the gynoecium indicate an origin in the euryplastic phase.

Alstroemeriaceae.

Herbaceous or lignifying, sometimes climbing plants, with the roots often tuberously thickened. The leaves twist often the petiols and turn the blade to the base as in *Luzuriaga* and some other families of this group. Flowers in apparent umbels or racemes. Often they have bracts at the base; solitary flowers are rare. They are hermaphrodite, actinomorphic, or one segment is somewhat different. Perianth in two 3-merous series, sometimes differentiated *(Bomarea)*. Stamens 6. Ovary inferior or semi-inferior, 3- or 1-celled. Ovules numerous. Fruit a capsule or berry. The family agrees in aspect and type of inflorescence with the dicotylophyll group; it is somewhat distinguished from this group by its large spathaceous bracts under the inflorescence and the great number of ovules. It is placed to the *Amaryllidaceae,* but represents evolutionarily an entirely different type, agreeing with the dicotylophyll group.

Philesiaceae.

Shrubs, undershrubs, often climbing, with thickened ramified rhizomes. Leaves broad, parallel or reticulately veined. Flowers hermaphrodite, actinomorphic, solitary or in apparent umbels or racemes, usually with scale-like bracts at the base. Perianth free or connate, sometimes differentiated into two different trimerous series. Stamens 6, free or a little cohering. Ovary 3- or 1-celled. Style one, with a capitate or 3-lobed stigma. Ovules numerous. Fruit a berry.

The *Philesiaceae* form a family which is considerably closely related to the *Alstroemeriaceae.* They differ from them only morphologically by the superior ovary. They were referred to the *Liliaceae* and represent one of the numerous evolutionary groups which do not belong to this family by their evolutionary trend. But also the *Alstroemeriaceae* do not belong evolutionarily to the *Amaryllidaceae* and were referred to these only by a questionable valuation of the nature of the ovary, irrespective of affinity. The *Philesiaceae* and *Alstroemeriaceae* should be united into one family, as they have very agreeing characters in common such as aspect, woody or herbaceous character, climbing types, shapes of the leaves, fruits, number of ovules, differentiated perianth, turning of the leaves, etc. The sympodial structure of the axis, the shape of the leaves, and their tendency to twist, the articulated pedicels make this family approach also to the *Polygonateae.*

Stenomeridaceae.

This monogeneric family is distinguished from the *Dioscoreaceae* only by unessential characters such as connectives produced into an elongated appendage with horned apex, many ovules superposed in each cell, hermaphrodite flowers, 3-partite styles, and long capsules. On the whole they do not deviate from the family *Dioscoreaceae,* and evolutionarily probably do not represent an independent isolated family.

Trichopodaceae.

Here belong two genera related to the genus *Stenomeris.* They are distinguished from it by the berry-like fruits with two ovules superposed in each cell, three to six stigmas, solitary flowers which are usually large in the genus *Avetra.* This family, too, cannot be regarded as an independent family as no essentially new evolutionary trend shows itself in it, but only some small modifications in the structure of the flowers and vegetative organs.

Roxburghiaceae.

Family distinguished from the *Dioscoreaceae* by dimerous flowers with four free petaloid segments in two series, 4 stamens with produced or also normal connectives, superior or semi-inferior 1-celled ovaries of two connate carpels, with two to many basal or apical seeds, and with capsules without wings.

This family with a very disjunctive area is important for an understanding of the relations of the *Dioscoreaceae* to the other families of the group. The dimerous flowers constitute a peculiarity, which occurs, however, also in some other representatives of this group *(Majanthemum, Aspidistra).* It represents a very ancient family, which maintained itself only in a small number of species and stands apart from the rest. In it many characters have been preserved which enable us to understand the relationship of the whole group, e. g. the produced and normal connectives, large flowers, superior to semi-inferior ovaries, etc.

Petermanniaceae.

Monotypical family with dicotyle leaves and climbing sympodial stems. Flowers hermaphrodite, with six almost free segments with deflexed lobes. Stamens six. Stigma capitate. Ovary inferior, 1-celled, 3-carpellate, with many ovules. Fruit a berry. The inflorescence turns sometimes into branched tendrils. A probably isolated type, by habit, inferior ovaries, and ovules in 2 series approaching the *Dioscoreaceae,* by perianth and stamens the *Smilacaceae,* by the sympodial structure of the axes *Luzuriaga,* and by the prickly stems the *Ruscaceae.* It is thus a type belonging to the dicotylophyll group. It has, however, a somewhat isolated position. Its occurrence is a relict one. Structure of the flower perfect.

Dioscoreaceae.

Climbing herbs or shrubs with tuberous rhizomes. In the stems there are sometimes vascular strands in cylinders. Leaves entire to digitately divided, alternate or opposite, petiolate, arrow-shaped, cordate, mostly digitately reticulately nerved. Flowers in racemose inflorescences, unisexual, rarely bisexual, actinomorphic, inconspicuous. Perianth of 6 segments in two series, most often connate. Stamen 6 in two series, connate at the base, sometimes one series developed as staminodes. Ovary inferior, 3-celled, with two ovules in each cell superimposed. Style one, stigmas three, often 2-parted. Fruit most often a winged capsule, rarely a berry.

This family occupies an extreme position among the Monocotyledons. It has numerous features in common with the Dicotyledons. They are, however, by no means characters which would not occur at least rarely also in other Monocotyledons; they are only more abundant in this family. The secondary thickening is effected by vascular strands in cylinders, but these have a monocotyle structure. The occurrence of two cotyledons has been observed also in other Monocotyledons, and also dicotyle leaves are not rare in the Monocotyledons.

In the *Dioscoreaceae* we observe a different evolutionary trend from that in the preceding groups. But this evolution shows also in families belonging to this evolutionary group. Often some of them are placed according to the structure of the flower to the *Amaryllidaceae* or to the *Liliaceae*. Their evolution went, however, in an entirely different direction, and they form an evolutionarily alien element in these groups. The formation of numerous modifications in the structure of the vegetative and generative organs and their disjunctive relict area show that the *Dioscoreaceae* are a very ancient family formed already in the euryplastic phase from an unknown, but certainly monocotyle stock. The affinity with the Monocotyledons is far better exhibited in the other families closely related to the *Dioscoreaceae*.

Summary: The dicotylophyll group is an example of an evolutionary group which had to be extracted from different places of the system. The system is built predominantly on the basis of the complicateness of the structure of the flower and not on the evolutionary trends, which were decisive for the differentiation of the individual families. On the basis of the herbarium material and of the taxonomic data the families have been selected in which the organs came to vary in a similar way, irrespective of the absolute size of the modifications. Attention was paid rather to the variation of the characters within well-defined taxons, and then only according to this the facility of a modification or its stabilisation was evaluated. Thus e. g. the position of the ovaries was not taxonomically valuated too highly as it changes easily. As an important character was valuated the tendency to form dicotyle leaves, woody climbers, tuberous rhizomes, produced connectives, umbellate inflorescences, etc. They are mostly characters which do not occur often among the Monocotyledons, and thus are more reliable for a valuation than characters which occur frequently in different evolutionary groups and sometimes also change easily. At the same time rather the presence than the absence of these characters was valuated. The occurrence of the characters mentioned at least in some members of the family was evaluated taxonomically very highly. On the other hand the absence of certain characters need not be too important, especially when it is compensated for by the presence of other characteristic features.

Most of the families belonging to this group have a stabilised structure of the flower, most often trimerous, pentacyclic, with a syncarpous ovary. Deviations are on the whole rare, as e. g. in the *Trilliaceae,* where there are a strong variation of the structure of the flower and the formation of pentacyclic flowers. Thus it seems that this family is one of the oldest in the group. But also this family exhibits a trend to form stabilised trimerous flowers. Also the *Aspidistraceae* have dimerous and trimerous flowers. The Roxburghiaceae have stabilised, but only dimerous flowers. Less often there is a variation in the number of some series in this group, e. g. the loss of one series of stamens *(Ruscaceae, Smilacaceae);* this trend shows also in the *Dioscoreaceae* in the formation of one series of staminodes.

The dicotylophyll group comprises the *Trilliaceae, Aspidistraceae* and *Taccaceae* as families of herbs, and the *Ruscaceae, Smilacaceae, Alstroemeriaceae, Philesiaceae, Dioscoreaceae, Stenomeridaceae, Trichopodaceae, Roxburghiaceae* and *Petermanniaceae* as families with a strong tendency to form woody climbers.

The Tepaloid Evolutionary Group.

This comprises a group of families with undifferentiated perianth and mostly pentacyclic, trimerous flowers with syncarpous ovaries. The differentiation of the individual families proceeded by small modifications in the structure of the flowers or by greater ones in the total aspect. It is characterised by the structure of the leaves, which are mostly linear and parallel nerved. Types with bulbs, corms and rhizomes are frequent.

Pontederiaceae.

Aquatic herbs reminiscent in aspect of some *Hydrocharitaceae.* Leaves opposite or verticillate, sheathing, parallel nerved. Flowers in spikes or panicles, growing from spathaceous bracts. They are hermaphrodite, actinomorphic, or moderately zygomorphic. Perianth imperceptibly 2-series, trimerous, free or cohering at the base, petaloid. Stamens 6, or 3, rarely 1. Ovary superior, 3 or 1-celled, with one to many ovules. Style one, stigma 1- to 6-lobed. Fruit a capsule or utricule. Endosperm mealy.

The position of this family is unclear. Most often it is referred to the affinity of the family *Liliaceae* because of the corolla-like developed perianth and the coherence of its two series. Often it is also placed to the family *Commelinaceae* because of the character of the androecium, the colour of the flowers, the symmetrical flowers, and the mealy endosperm. Evolutionarily it corresponds, however, fairly well to the family *Hydrocharitaceae,* with which it has some characters in common (sheaths under the scapes, general habit, the genus *Hydrotrix* shows the variability of the *Helobiae*). Others are, however, very different. Sometimes it is placed between the *Liliaceae* and *Commelinaceae* as a transitional family. Notwithstanding the relatively stabilised flower it shows many, rather rare characters such as a sympodial structure of the stems, submerged and floating leaves differentiated in *Heteranthera,* swollen petioles as floating device in *Eichornia,* fruits enveloped by a perianth, heterostyly and kleistogamy. Its great variability and pantropical distribution show that this family arose in the euryplastic period. It is not excluded that it is a parallel type of the family *Hydrocharitaceae* with superior ovaries. It has many characters in common with this family. Evolutionarily the *Pontederiaceae* stand somewhat apart, but they may represent one of the basic possible types of the tepaloid group as do the *Hydrocharitaceae* in the sepaloid group. Their evolution is, however, already far more stabilised, nor are there any longer such great modifications in the structure of the flower.

Hypoxidaceae.

Herbs, often with tuberous rhizomes. Leaves mostly basal, linear or lanceolate, parallel nerved, flowers hermaphrodite, actinomorphic, in racemose inflorescences on leafless scapes. Perianth free or connate in a long beaked tube, 6-merous, often outside hairy. Stamens 6, rarely 3. Ovary inferior, 3-celled. Styles 1 or 3. Ovules numerous. Fruit a capsule or berry.

Small family belonging to the affinity of the *Haemodoraceae*. The structure of the leaves and stems corresponds to the structure of many other liliaceous species. By these characters, too, it belongs to the tepaloid group.

Velloziaceae.

Trees or shrubs. Leaves linear, crowded in the tufts at the ends of the branches. Flowers actinomorphic, hermaphrodite, solitary. Perianth of two trimerous series, free or connate, persistent. Series sometimes distinguished by a different hairiness. Stamens most often 6 in two series. Rarely multiplied to six clusters of 2 to 11 stamens each *(Vellozia, Breviscapa)*. Ovary inferior, 3-celled. Ovules numerous on axile stalked placentas. Style one, capitate, or 3-branched. Endosperm abundant.

Small family, sometimes referred to the *Amaryllidaceae*, sometimes to the *Haemodoraceae*. The evolution of this family had, however, a different trend from that of these two families. Woody stem dichotomically ramified, multiplication of stamens, stalked placentations, and very disjunctive distribution characterise this group. It is probably a very ancient group, which originated in the euryplastic phase. But it became soon stabilised and did not form many types. It seems to be most closely related to the Haemodoraceae, and has also a similar area.

Haemodoraceae.

Herbs with fasciculate roots, corms or rhizomes. Leaves mostly basal, linear. Flowers hermaphrodite, actinomorphic or zygomorphic, in cymes, racemes, panicles or heads. The pedicels have prophylla. Perianth undifferentiated, persistent, 6-merous in one series, free or connate. Stamens three, rarely 6. Ovary inferior, semi-inferior, or superior, 3-carpellate. Style usually filiform, stigmas often three. Fruit a capsule. Ovules one to many. Endosperm abundant.

Small family, evolutionarily homogeneously defined by Hutchinson. Because of some transitional characters in the structure of the flowers, e. g. in the position of the ovaries, the suppression of one series of stamens, it was often artificially divided, and some of its members were placed to the *Amaryllidaceae*. This family shows us that it is not possible to use for the division of the families only some of the principal characters in the structure of the flowers. Also the characters of the vegetative organs and the other details have to be taken into account. The principal characters can be used only in an artificial system where the aim is a quick placing and determination of a plant. Just this family offers examples of how easily the position of the ovary changes in closely related types and often even within the same genus. Also the loss of one series of stamens is not unusual in the Monocotyledons and occurs in all evolutionary groups. Thus this character cannot be used as an important criterion.

The great variation of the individual organs of the flower, the one series of the 6-merous perianth, the different types of the inflorescence, the pronounced hairiness indicate that this family originated in the euryplastic phase. But in the stenoplastic phase it did not undergo any great differentiation into many genera and species. Also the distribution of the family is a relict one, and it is mostly restricted to the southern hemisphere. Evolutionarily this family stands somewhat apart from the other families of this evolutionary group. By some characters and in habit it approaches the *Orchidaceae*.

Tecophilaeaceae.

Herbs with rhizomes or corms. Leaves linear to orbicular ovate. Flowers hermaphrodite, actinomorphic, in racemes or panicles. Perianth connate at the base, rarely free. Stamen 6, but mostly 3, rarely 4 fertile and 3 or 2 as staminodes. Ovary semi-inferior, 3-celled. Capsule with numerous seeds and abundant endosperm. The perisperm reported from *Cyanastrum* proved according to Fries and Nietsch to be a tissue formed by the proliferation of the cells of the chalaza after fertilisation.

This family, defined by Hutchinson, is quite natural. It has a very disjunctive area, indicating the great age of the family. The structure of the ovary is on the transition between the families *Iridaceae, Amaryllidaceae* and *Liliaceae.* Thus it shows also some relations to the genera *Peliosanthes, Ophiopogon,* etc. of similar structure, and also to the *Dianelleae.* Evolutionarily it represents a lateral group of the family *Liliaceae* with a somewhat greater variation in the androecium.

Agavaceae.

Plants with rhizomes and with well developed stems, thickening secondarily. Leaves narrow, parallel nerved, rarely pinnately nerved *(Cordyline)*. Flowers hermaphrodite, polygamous, or unisexual, actinomorphic or zygomorphic, in racemes or panicles. Rarely solitary flowers *(Pseudobravoa)*. Pedicels sometimes articulated. Perianth free or connate. Stamens 6 in two series. Ovary inferior or superior, 3-celled. Seeds one to many in each cell. Fruit a capsule, often winged, or a berry.

This family was defined by Hutchinson by uniting the *Dracaenoideae*, separated from the *Liliaceae*, and the *Agavoideae*, separated from the *Amaryllidaceae*. It is characterised by aspect and ecology. The cytological analysis indicates the homogeneity of this group. The *Agavoideae* and the *Yuccaceae* have the same, but on the whole peculiar number of chromosomes. There are in them 5 broad and 25 small chromosomes. This proves clearly that the *Agavoideae* belong to this family, just as the genus *Polyanthes*, which has the same number of chromosomes. In other genera which belong here, the mutual affinity is evident from the similar morphological structure although they have a different number of chromosomes. The agreement between *Agave*, *Yucca*, and *Polyanthes* indicates a common origin of this group. The occurrence of such a number and shape of the chromosomes is unusual in plants. It cannot be attributed to parallel evolution. Also the aspect, secondary thickening, and ecological character indicate a close affinity of these types and common ancestors. The affinity to the family in plants. It cannot be attributed to parallel evolution. Also the aspect, But also some genera of the family *Bromeliaceae* have a very similar aspect. The *Xanthorrhoeaceae* are distinguished especially by their membranaceous perianth and the independence of each series of the perianth. Thus they differ essentially from the *Agavaceae* as well as from the *Liliaceae*. They agree with the xeranthemous group.

Iridaceae.

Herbs, rarely undershrubs. Mostly with rhizomes, corms or bulbs. Leaves narrow, most often distichous. Flowers hermaphrodite, actinomorphic or zygomorphic. Perianth petaloid, of 6 segments in two series, sometimes differing in size. Stamens three, rarely two *(Diplarrhena)*, free or connate. Ovary inferior, rarely superior, 3- or 1-celled. Styles 3-branched, often divided. Ovules one to many. Fruit a capsule, sometimes with a scar at the end. Seeds with endosperm.

The *Iridaceae* form a large group of plants related to the families *Liliaceae* and *Amaryllidaceae*. They are distinguished from them by relatively peculiar features, such as by the formation of only one series of stamens, and by styles with a tendency to ramify. The evolutionary trends are here therefore somewhat extreme. It comes here also to an absolutely extreme configuration of the bracts under the flowers. One of these bracts is often 2-keeled as in the palea of the *Gramineae*. This was probably caused in the ontogeny by the pressure of the adjoining axis. This causes a division of the main rib into two prominent nerves. In the terminal flowers, however, this sometimes does not occur, just as in the *Gramineae*. Then both bracts are mononerved. The occurrence of this feature in two such different evolutionary groups is very remarkable, especially as it is an important taxomic character. Also the inflorescence is in the *Iridaceae* rather extremely developed. Thus it is not surprising that the whole family was from an evolutionary point of view always defined far more homogeneously than the *Liliaceae* and *Amaryllidaceae*. In these as perfect predisposed prototypes evolution could aim at the formation of the same structure of the flower in different evolutionary groups. In the *Iridaceae* by the peculiar deviation from this evolution it was already less probable that two different evolutionary groups should have the same structure of the flowers and inflorescences. This does not mean of course that this family would have to be absolutely homogeneous. Even when the evolutionary trend is peculiar there may occur homologous variability in so closely related groups. Some types of the *Iridaceae* can have the evolutionary trend of this family weakened, and on the contrary some types from the *Liliaceae* and *Amaryllidaceae* can have a rarely developed trend towards flowers similar as in the *Iridaceae.* In these cases the placing of such morphological transition types may cause difficulties, as we see in some transition types. Thus types with 3 stamens or 3 fertile stamens and 3 staminodes occur in the *Liliaceae* as well as in the *Amaryllidaceae.* An example is given by the *Cochicaceae,* where the *Crocoideae* form 3 stamens, branched stigmas, but not the characteristic bracts under the flowers; rarely there occurs also a second series of stamens. Also the resemblance of some species of the genera *Aristea* and *Aphyllanthes* may indicate affinity. The family *Amaryllidaceae* shows also many types which are very close to the family *Iridaceae,* e. g. most types with one flower differ sometimes only by the development of two series of stamens.

This family shows also a differentiation of the leaves into most of the basic shapes which we observe in the main evolutionary groups of the Monocotyledons. Sometimes this occurred also in genera, e. g. in the genus *Babiana.* Here there are most often linear leaves, parallel nerved, and mostly with numerous transverse nerves. In *B. cuneifolia* we see the origin of a digitate leaf similar to that of some palms. All the nerves above the contracted petiol diverge fan-like in the blade. Thus a broadly triangular blade is formed, which is crenate at the end, with shallower and deeper lobes. *B. fimbriata* has narrowly linear leaves, but produced at the end of the midrib and spirally turned as in *Fritillaria* and *Gloriosa.* Frequent are also duplicately folded leaves composed of alternating thinner and thicker ribs. Sometimes they are asymmetrical, or the thickest rib sits at one margin and one-sidedly secondary nerves start from it. In other species the nerves separate from the thick midrib to both sides, thus giving a pinnately nerved blade. Thus we have here within one genus most of the basic leaves which are often characteristic for whole evolutionary groups. This is an example of equal modifications, taxonomically of very different importance. In the genus *Gissorhiza* it came e. g. in G. *rupestris* to the formation of reticulately nerved leaves, though most of the species have parallel nerved leaves.

The world-wide distribution of the *Iridaceae* with their main centre in America and South Africa indicates their very ancient origin. Also the different deviating basic types indicate an origin in the euryplastic phase and a rich disintegration in the stenoplastic phase into many genera and species. The genera *Libertia* and *Orthosanthus,* distributed in Chile and Australasia, must have originated at a very early time, as they must have extended their area at the time of the connection of these continents. They indicate one of the oldest disjunctions known in the Angiosperms.

Amaryllidaceae.

Herbs, mostly with bulbs or more rarely with rhizomes. Leaves narrow, parallel nerved, rarely cordate, petiolate *(Eucharis)*. Flowers large, hermaphrodite, actinomorphic, rarely faintly zygomorphic, in umbels composed from cymes. Usually one or more bracts at the base. Perianth petaloid, undifferentiated, 6-merous in two series, rarely trimerous *(Trichlora)*, free or connate. Often a corona is developed. Stamens 6, rarely multiplied, or 3 and another 3 as staminodes. Ovary superior or inferior. Ovules numerous in 2 superposed series. Fruit a capsule or berry. Seeds with endosperm.

The *Amaryllidaceae* are defined by different authors more narrowly or more widely. Some authors include here all types related to the *Liliaceae* which have an inferior ovary. Thus there is formed an evolutionarily inhomogeneous group comprising the *Amarylloideae, Agavoideae, Alstroemerieae, Hypoxideae, Conanthereae, Conostylideae* and *Campynematoideae*. It has been demonstrated, however, that the mere position of the ovary is not able to define a related group. It is necessary to find some other characters which will make it possible to form evolutionarily homogeneous groups. Therefore Hutchinson defined this family far more narrowly according to the nature of the inflorescence. He excluded most of the other types, and added corresponding types from the *Liliaceae*. Thus a homogeneous group was formed, defined by umbels composed of cymes with bracts at the base. The ovaries were here inferior and superior. We find here often striking morphological convergences, which may sometimes indicate more than mere parallel evolution. In the *Liliaceae* attention was drawn to the possibility of forming an independent family *Colchicaceae*. There may be more such cases. Thus *Calochortus*, which causes some taxonomic difficulties, resembles the genus *Ixiolirion*, whose position among the *Amaryllidaceae* is isolated. Also *Gagea, Lloydia, Nothoscordum,* and *Muila* show a certain agreeing configuration. Also the position of some types showing a tendency to a restriction of the stamens to one series is still unclear.

The *Amaryllidaceae* in the sense of Hutchinson are a rather homogeneous family. They are distributed throughout the world. This indicates their origin at the time of great evolutionary vigour. In the stenoplastic phase they formed in certain regions a number of genera mostly confined to one phytogeographical region.

Liliaceae.

Herbs, rarely undershrubs, or shrubs of very varied aspect. Leaves mostly parallel nerved. Frequent bulbs, corms, or rhizomes. Flowers solitary, in spikes, racemes, or panicles, of very uniform structure. They are hermaphrodite, actinomorphic, rarely faintly zygomorphic. Perianth coloured, undifferentiated, in two series, free or connate. Stamens 6 in two series, rarely 12 *(Pleea)*. Ovary tricarpellate, connate, superior to semi-inferior, one- to three-celled. Often the carpels are only imperfectly cohering. Styles one to three, stigma one or three. Fruit a capsule, rarely a berry.

The *Liliaceae* formed a considerably heterogeneous group. Types were placed here, very similar in the structure of the flower, but certainly different in relationship. More recently, after more detailed study, Hutchinson separated the following families from the *Liliaceae: Ruscaceae, Philesiaceae, Smilacaceae, Dracenoideae, Agapantheae, Allieae, Gilliesiae, Trilliaceae, Petrosaviaceae, Xanthorrhoeaceae* and *Tecophilaeaceae.* Nevertheless there remained in the *Liliaceae* a great number of different types. Some have very characteristic features and often form small, isolated groups. They seem not to have been fully investigated taxonomically. The *Liliaceae* afford an example of a family which has been gradually taxonomically sifted. In some systems the chief emphasis is laid on the characters in the structure of the flowers and far less on the characters of the vegetative organs. At most the taxons lower than the families were defined by them. As the whole evolution of the Monocotyledons seems to be governed by evolutionary predisposition to trimerous, pentacyclic flowers with syncarpous ovaries it is natural that these types represent the most frequent terminal evolutionary stages. They may, however, occur also in some other evolutionary groups. Here the structure of the flower may often agree fairly much in all features. Trimerous, pentacyclic flowers indicate in such cases a certain common evolutionary stage, but not any relationship. Hence we find the formation of such a heterogeneous complex in the family *Liliaceae.* Even though Hutchinson's emendation seems to be fully justified, yet we find in the rest still many heterogeneous types whose characters have an entirely different evolutionary sense than the main part of the representatives of this family. Often they are little numerous groups, which do not harmonise with the main group to which they are placed.

In the group *Heloniadeae* there occurs an evolutionary character rather alien to the whole rest of the family with the exception of the genus *Lilium.* They have leaves with dicotyle nerves, usually in rosettes at the base of the stems and only bract-like on the stems. Flowers in a long raceme, inconspicuous, with persistent perianth. Ovaries mostly only imperfectly connate; they have mostly three styles or one three-branched style. There occur here hermaphrodite and dioecious, actinomorphic and zygomorphic types, several to many ovules in the carpels. Also the shape of the pollen is rather different in the different representatives. They are mostly types of humid habitats. It is not excluded that this group is somewhat parallel to the family *Scheuchzeriaceae.* Both groups are of a very similar evolutionary valence, and were differentiated in a similar way, and may also have common ancestors. The other *Liliaceae* probably did not arise from them, and they stand rather apart. Thus it seems preferable to leave this group independent.

The following types are evolutionarily on the whole rather homogeneous: the *Narthecieae, Asphodeleae, Veratreae, Kniphofieae, Heme-*

rocallideae, Aloineae, Uvularieae, Tricyrtideae, Tulipeae and *Scilleae.* These types separated probably already in the euryplastic period, and in the later stenoplastic period each group differentiated into a number of similar genera. According to the rate of decrease of the evolutionary vigour and to their ability to maintain themselves in nature there appear in the individual groups larger or smaller modifications and a greater or smaller number of species. The structure of the flower is in the large majority of representatives very stable, and exceptions occur only very rarely. They occur mostly in types whose placing in this family is rather doubtful. Thus semi-inferior ovaries occur in *Mondo, Ophiopogon, Aletris, Peliosanthes, Hemerocallis,* multiplied stamens in *Pleea,* a corona in *Diasporopsis,* a perianth differentiated into two different series in *Lachenalia, Albuca, Daubenya.*

The *Narthecieae* have the simplest structure. Some types resemble and perhaps are also related to the genus *Triglochin.* They are not only habitually similar to it, but have also a similar structure of the gynoecium. Carpels only little cohering. It is a very ancient group with disjunctive areas. The 3-lobed calyculus under the flowers of the genus *Tofieldia* is reminiscent of the bracts of the *Iridaceae,* and is entirely alien to the family *Liliaceae.* It may be doubtful whether this genus belongs to the family, especially as also *Isophyssis* with a superior ovary is placed in the family *Iridaceae.* Also the genus *Nietneria* with a semi-inferior ovary shows a tendency towards the *Iridaceae.* The distichous position of the leaves, rare in the *Liliaceae,* is also peculiar.

The *Asphodeleae* represent the basic evolutionary group of the *Liliaceae.* It is again a very ancient group, differentiated into a number of types distributed throughout the world. Some types placed here are taxonomically problematic and show close relations to other families. Thus *Thysanotus* has bracteoles under the flowers, and in the stamens the inner series sometimes aborts as in the family *Iridaceae.* The frequent occurrence of articulated pedicels is also intresting in this group. Sometimes the articulation looks as if a long carpophore was growing from the node, by whose shortening an inferior ovary might originate.

The genus *Aphyllanthes* is evolutionarily considerably alien to the family *Liliaceae* by its aspect as well as by the bracts under the flowers. It belongs in the affinity of the *Xanthorrhoeaceae* of the xeranthemous group.

Herreria belongs probably to the family *Ruscaceae,* to the affinity of the genus *Asparagus.* It has in common with this genus climbing stems, cladode-like leaves in clusters, articulated pedicels, small subtending bracts, etc.

The *Mondoideae* and *Aletroideae* are probably evolutionarily fairly closely related. They show certain relations to the *Narthecieae*, but have semi-inferior ovaries.

The *Johnsonieae* do not belong at all to the tepaloid group; together with the *Xanthorrhoeaceae* they are closely related to the family *Eriocaulaceae.*

The *Aspidistreae* are evolutionarily alien to the *Liliaceae* and *Ara-*

ceae. They exhibit many peculiarities unusual in this family, such as 4-merous flowers, axillary scapes with bracts, pulpy perianth, large broad styles and stigmas, often 1-seeded berries. The evolutionary trend which shows itself here is, however, very similar to that in the family *Taccaceae.* They stand, however, somewhat isolated, and it is necessary to separate this group as an independent family which is, however, most closely related to the *Liliaceae,* from which it is distinguished by the inferior ovary, the numerous ovules, etc. The relations to the *Araceae* do not seem to be direct, as the only common character is the fleshy, thick spike, of course without spathe. Thus it is very probably a convergent and not an affinity character. A spathe reminiscent of that in the *Araceae* is developed in *Milula,* but also this genus is not related to the *Araceae.*

Most of the species of the *Polygonateae,* especially the species with flowers in umbels show a close affinity with the family *Ruscaceae,* with which they have also a similar evolutionary trend. They should certainly be placed rather in the *Ruscaceae* than in the *Liliaceae.* They show also a tendency to articulated flower pedicels, etc. *Polygonatum* shows, however, closer relations to the *Liliaceae,* and especially to the *Uvularieae.*

The *Dianelleae* are a small, very ancient group, distributed in almost all continents. Though it is little different from the *Asphodelleae,* yet its position may be more independent. Only the similar structure of the flower and on the whole little marked specific character make it impossible to establish it as a separate family. It shows close relations to the family *Tecophilaeaceae.*

The *Anguillarieae* and *Iphigenieae* are groups somewhat related to the *Veratreae. Androcymbium* seems to be different not only in aspect but also by the pollen. It belongs probably to the *Colchicaceae.*

The *Massonieae* constitute a rather strange type with the flowers in bracteate heads, with some sterile bracts at the base. The flowers unfold from the rim. They seem to have a parallel evolution to that of the family *Amaryllidaceae.* In the genus *Daubenya* the outer segments of the perianth are long, the inner ones short. This character is exceptional in the *Liliaceae.*

The genus *Asparagus* belongs by its whole evolutionary trend among the *Ruscaceae.* To separate it from this family would be rather forced.

The *Bowieae* form a small group of three genera with a very characteristic evolutionary trend. The formation of corms and bulbs and the leaves of different shapes (mostly soon disappearing), the green, ramified, often climbing stems, and the small greenish flowers show that it is a relict group. It is not excluded that it could be raised to an independent family. Even if it did not come here to any essential modification in the structure of the flower, yet the general character is essentially different from that of the other *Liliaceae.* Nor does it seem to have common ancestors with the family *Liliaceae.*

The taxonomic position of the *Colchiceae* is interesting. The habit of this group is very characteristic and shows a striking resemblance to that of the group *Croceae* among the *Iridaceae.* Also some genera of the *Amaryllidaceae,* such as *Sternbergia, Gethyllis, Apodolyrion,* are similarly configurated. All differ, however, from each other by the essential characters by which the families are distinguished in which they have been placed. Their differences are, however, not basic ones. Neither an inferior or superior ovary, nor the development of one or two series of stamens need invariably be a reliable distinguishing character. Thus there arises here the question whether we have a convergence caused by the material predisposition of the whole group or a true relationship. The detailed analysis of all these genera shows that it is not excluded that they might belong to one evolutionary group. If so, then the *Colchicaceae* would of course form an independent group characterised by habit, mode of life, and morphological structure. It is only the emphasis on the character of the ovary which has led to the splitting up of this group and its division into different families. But the extreme characters in common should count for more than mere evolutionary convergence. This case seems to be similar to that of the family *Amaryllidaceae* defined by Hutchinson. In abnormal cases also an outer series of stamens was observed in the genus *Crocus*.

Lloydia, Calochortus and *Gagea* have a somewhat unclear position. *Lloydia* has flowers of which the terminal flower develops first and the lower axillary ones later. By this character it differs from most of the *Liliaceae*. Besides there are here sometimes polygamous flowers. Thus in *L. graeca* the terminal flower is hermaphrodite, only the lower two are male. In this character this type agrees with the genus *Gagea*, where similar flowers and inflorescences occur. In *Calochortus* the inflorescence is often still more complicated. The lower bracteate branches flower later than the two terminal flowers. But in these terminal, almost opposite flowers there first grows the flower from the axile of the lower bract. Thus all three genera differ in the structure of the inflorescence from the remaining related *Liliaceae*. They should probably form an independent group to which would belong evolutionarily also the genus *Ixiolirion* from the *Amaryllidaceae*.

After excluding the types probably not belonging to the *Liliaceae* we see in these several basic types. The *Narthecieae* seem to be the simplest type. The family reached its maximum expansion in the groups *Asphodeleae* and *Scilleae*. All in all the following four groups of related types can be distinguished:

(1) *Asphodeleae, Narthecieae, Veratreae, Anguillarieae, Iphigenieae.*
(2) *Aloineae, Kniphofieae, Hemerocallideae.*
(3) *Uvularieae, Tricyrtideae.*
(4) *Scilleae, Tulipeae.*

Around these there are more or less related types of small groups, distinguished in minor characters, such as e. g. the *Dianelleae, Massonieae, Mondoideae* and *Aletroideae*.

Summary: The tepaloid group comprises many types with a very similar structure of the flowers, but these types differentiated into fairly well definable groups. All families represent the terminal members of an evolutionary differentiation in which the structure of the flowers predisposed in the Monocotyledons was reached. The differences in the individual groups are according to the structure of the flowers undefined. Inferior and superior ovary, reduction of the stamens occur to a greater or lesser extent in all families. Thus it is not possible to use these characters as good criteria. Hence all the other characters and properties have to be taken into account in order to obtain families with a homogeneous trend of evolution. Neither is the type of the inflorescence an absolutely safe character, as can be seen in *Calochortus, Lloydia,* etc. Also the shape of the pollen varies rather considerably as it does in most of the families formed in the euryplastic phase and oriented to several evolutionary trends. In some doubtful cases it may, however, enable us to reach a correct solution. For the distinction of the families it is therefore necessary to use all available characters. Especially the direction and quality of the evolution have to be considered rather than details. For this purpose the erection of small, but well homogeneous families is more suitable. From this point of view some families as e. g. the *Liliaceae* are even after the exclusion of many types still too big and perhaps also too heterogeneous.

An interesting feature of this group is that its differentiation is not directed in a definite direction. All families are regularly grouped around the basic structure of the flower. The differentiation sets in on the whole in more subordinate characters, and the total aspect is often a good character. It may very often correspond well to certain evolutionary trends.

The whole group is characterised by the relatively constant feature of a perianth undifferentiated into calyx and corolla, formed tepaloid. Although in some types there are deviations from this evolution, as e. g. in the types with a differentiated outer and inner series of the perianth, a typical calyx was never developed. Rather can here be seen the opposite trend, a reduction of the two series into one. This trend of evolution shows most perfectly in the *Haemodoraceae,* where there is no differentiation at all of an outer and inner series of the perianth. The types exhibiting a great independence by the evolution of two series, as in the family *Xanthorrhoeaceae,* appear as alien elements in this evolutionary group, and have to be excluded from it. An on the whole homogeneous evolutionary trend seems to manifest itself in all families included here. They are the following families: *Pontederiaceae, Liliaceae, Amaryllidaceae, Iridaceae, Agavaceae, Tecophilaeaceae, Haemodoraceae,* and *Velloziaceae.* The *Pontedericeae* are the simplest and may link themselves to the *Helobiae.*

The Anomalous Evolutionary Group.

This group comprises families with a very varied structure of the flowers. The common feature is the tendency to form bizarre shapes and extreme biological properties. The tendency to form saprophytic and sometimes also parasitic, non-chlorophyl types is important. Here belong eight families which except for the *Orchidaceae* are rather rare.

Triuridaceae.

Small saprophytic herbs. Flowers small, in bracteate cymes, monoecious, dioecious, rarely polygamous. Perianth petaloid, 3- to 8-merous in one series. Stamens 2—6, often 3 staminodes and 3 fertile. They are 2-, 3- to 4-celled. Gynoecium composed of many free carpels with terminal but also basal styles. Ovules solitary, basal, with one integument. Seed with the embryo not differentiated and abundant endosperm. Small family, which is most often referred to the *Helobiae*, with which it has, however, nothing in common except the apocarpous gynoecium. It exhibits much rather an evolutionary trend similar to that in the *Thismiaceae* and *Burmanniaceae*. The characters in common are the saprophytic character, the strange long appendages on the perianth, the tendency to trimerous flowers, mycorrhiza, sympodial and racemose inflorescences, anthers immersed in the receptacle, embryo not differentiated, produced connectives, undifferentiated perianth, etc. On the other hand it is distinguished from the *Thismiaceae* and *Burmanniaceae* essentially by the solitary flowers, the undefined structure of the flower, the superior apocarpous gynoecium, and the solitary ovules with only one integument, as the inner integument is later reabsorbed. The unstable structure of the flower and the wide disjunctive area indicate that this family originated very early in the euryplastic phase. It is possible that it has common ancestors with the *Burmanniaceae* and the other families of the anomalous evolutionary group. By its evolutionary trend it certainly fits best into this affinity.

Petrosaviaceae.

Monotypical saprophytic genus without chlorophyl. Flowers hermaphrodite, actinomorphic, in racemose inflorescences. Perianth in two morphologically differentiated, 3-merous series. Stamens 6. Carpels 3, almost free. Ovules numerous. Strange species referred to the *Liliaceae* or *Scheuchzeriaceae*. It seems, however, that also for this species a placing in the anomalous evolutionary group is not improbable. It seems to be related most closely to the family *Triuridaceae*.

Philydraceae.

Herbs with linear, basal and cauline leaves. Flowers zygomorphic, solitary, composing a spike or a panicle of spikes. Perianth petaloid, 4-merous, free, in two series. Stamen one. Ovary superior, almost 3-celled, 3-carpellate, with numerous ovules. Stigma simple. Fruit a capsule, or dry, indehiscent.

Small family, most often referred to the *Commelinaceae* or *Pontederiaceae*. Hutchinson placed it to the *Haemodorales*. Its taxonomic position is not too clear. There are mostly no representatives in our herbaria, so that this affinity could not be proved. It seems, however, that the great disturbances in the structure of the flower symmetrical flowers, leafy stems, parallel nerved leaves, numerous ovules, and petaloid perianth agree fully with the evolutionary trend which shows itself in the anomalous evolutionary group.

Apostasiaceae.

Rhizomatous herbs with petiolate, parallel nerved leaves. Flowers hermaphrodite, actinomorphic or slightly zygomorphic. Perianth of

6 free segments. Stamens 3, one of the outer series and two of the inner one, or only two of the outer series. Filaments united with the style. Ovary inferior, 3-celled, with many ovules. Fruit a capsule. Seeds small. Because of many similarities this small family was mostly referred to the *Orchidaceae*. More recently it has been separated as independent. It is distinguished in the main only by the almost actinomorphic flowers. It is probably only an extreme case of the family *Orchidaceae*.

Burmanniaceae.

Small saprophytic and green herbs growing in moist tropical forests. The sarcophytic herbs are rhizomatous, without chlorophyl, rootless, with the leaves reduced to scales. The green types have linear, lanceolate leaves in a basal rosette and often also on the stems. Flowers in racemes, cymes, or solitary. Perianth petaloid, tubular, 6- or 3-lobed. Stamens 3. Connectives wing-like broadened. Pollen free. Ovary inferior, 3- or 1-celled, 3-carpellate. Ovules numerous, small. Fruit a capsule. Seeds with embryo not differentiated and scanty endosperm.

Small family with a world-wide distribution and often disjunctive areas. This and the great morphological modifications indicate its very ancient origin. The morphological structure of the family as the reduction of the stamens, the broadened connectives, the biology, small seeds, embryo not differentiated indicate an affinity with the *Thismiaceae, Corsiaceae* and *Orchidaceae*. The genus *Burmannia* with saprophytic and normal types is evolutionarily important.

Thismiaceae.

Saprophytes without chlorophyl, with solitary, actinomorphic flowers, but of bizarre structure. The tubular corolla is 6- or 3-lobed and has long filiform appendages. Stamens 6, rarely 3. Ovary 1-celled, with three parietal placentas, which break away. Ovules numerous. Capsule with small seeds without endosperm.

With regard to relationship it stands closest to the families *Burmanniaceae* and *Corsiaceae*. With the other families of this group it has morphologically relatively little in common. Evolutionarily, however, it shows a similar trend in the modification of the basic structure of the flower, such as the reduction and bizarre configuration of some flower parts, the tendency to saprophytism, etc.

Corsiaceae.

Small, saprophytic and sometimes also parasitic plants without chlorophyl. Flowers solitary, zygomorphic, with the posterior segment of the perianth spade-like enlarged and the other 5 filiform. For the rest this family agrees with the preceding one. By its bizarre zygomorphic flower it resembles considerably some species of the family *Orchidaceae*, but is distinguished from it by the 6 stamens. It is related to the families *Burmanniaceae* and *Thismiaceae*, with which it has probably a common origin.

Orchidaceae.

Terrestrial, epiphytic and saprophytic plants with parallel or reticulately nerved leaves. Roots, stems and leaves of the most varied shapes and functions. There are normal, aerial, assimilating, tuberous roots, sometimes no roots are developed at all. Stems leafy, without leaves, climbing, creeping, tuberous, fleshy, articulated. Leaves entire, alternate, opposite, orbicular, linear to broad, ensiform *(Oberonia, Maxillaria),* isolateral *(Trizeuxis),* riding *(Notylia, Plectrophora),* articulate, reduced to scales, persistent, dicotyle *(Nervilia, Chlorosa, Calypso, Chrysoglossum,* etc.), whorled *(Codonorchis),* whip-shaped *(Scutinaria),* etc. The flowers are of bizarre shapes, in racemose inflorescences. They are zygomorphic, actinomorphic, hermaphrodite, rarely polygamous, monosexual, or sterile *(Oncidium ornithocephalum).* In some species there are different types of flowers. Perianth petaloid, of 6 segments in two series, many shapes and sizes. Especially labellum is sometimes very bizarre. Stamens in two series, but usually only one or two are developed, and the others are absent or are present as one or two staminodes. Pollen granulose, often agglutinated into pollinia. Ovary inferior, of 3 carpels, 1- or 3-celled. Stigmas 3 or 2, and the third changed into a rostellum. Ovules numerous, small. Fruit a capsule, rarely a berry *(Cyrtosia).* Seeds without endosperm, embryo not differentiated.

The characters are given only briefly, and it is not possible to give details. But even so it will be clear how great is the diversity of all the organs and their parts. This shows itself most markedly in the flowers. Though they preserved the characteristic zygomorphy, yet the individual parts are mostly different in shape from the parts in the other Monocotyledons. Nevertheless the basic structure of the Monocotyledons is preserved, but it is affected by anomalous modifications. Many parts do not retain their normal function, and the whole flower is strangely deformed. Notwithstanding the complexity of pollination a wealth of genera and species was formed. This is due probably not only to the great evolutionary vigour but also to the evolutionary lability due to the tendency to form irregularities. This carries with it an easy differentiation of the types, even when only a small deviation from the original types results.

Though the variability of this family is enormous, yet it is by no means undirected, and some characters remain at least qualitatively the same, and then they become characteristic for this family. Such characters are the zygomorphic flowers, the racemose inflorescence, the tepaloid perianth, one to two fertile stamens, granular or agglutinated pollen, very numerous seeds without endosperm, embryo not differentiated, etc. The complex of these characters characterises well this group. But there are still other characteristic features. Thus the differentiation into a terrestrial, epiphytic and saprophytic mode of life. Especially the tendency to saprophytism is an important character, as the Monocotyledons do not include any plants without chlorophyl except for this group.

This vast group arose by the most varied differentiations of the structure of the flower, leading to very remarkable configurations, of the mode of life and of the aspect. In this group a case of evolutionary processes has probably been preserved as they took place in the euryplastic phase. Today this family is probably like the other types in a pseudoplastic phase. But some characters and properties of the time of high evolutionary vigour have become stabilised. Thus from these we can form an idea of how such a process took its course. In the differentiation of this family the very interesting genetic ability has been preserved to interbreed also with dissimilar types. On the basis of the morphological structure the systematicians often separate such types into separate genera and often also higher taxons. This family shows how the point of view of classical morphology is often upset by nature, and consequently has to be changed. This family shows that morphological non-affinity is sometimes only apparent, and that closely related types may be morphologically very different. It looks as if the euryplastic evolutionary vigour, in which such phenomena were probably current, had stabilised itself here. At that time the species might be so plastic that this plasticity compensated also for apparent great genetic deviations. Most of the species later lost this ability, and today mostly only very closely related types can interbreed.

Interspecific hybrids, though known also in other families, yet arise always from species on the whole rather similar to each other. Nowhere else do we find so great an intergeneric hybridisation as in the *Orchidaceae*. The most interesting here are the trigeneric hybrids of the genera *Cattleya, Brassavola* and *Laelia,* which are recognised as good genera. But no barrier of sterility is developed between them. They interbreed within the genus and between the different genera. Many trigeneric hybrids are known, designated as *Brassocattlaelia.*

There is, however, still one more remarkable property, which indicates conditions in the euryplastic phase and which is probably connected with the first phenomenon. The shapes of the flowers need not be decisive for the genetic affinity. Some species form morphologically very modified shapes of flowers on one plant. The types in which such modified flowers grow on different specimens have often been referred even to different genera. Such a diversity of the flower distinguishes the genera *Catasetum, Oncidium,* and *Renanthera.* These genera, in which sometimes different types of flowers occur on one plant, enable us to explain also the frequent intergeneric hybrids in this family, as sometimes we have here a closely related type, which, however, bears one type of flower, whereas the related "genus" has another type of flower. Such phenomena may have occurred quite frequently in the euryplastic phase.

The vast distribution, disjunctive areas, morphological diversity indicate the great age of the family and the long conservation of the evolutionary vigour. The tendency not to form an endosperm, the modifications in the structure of the flower, the small and numerous seeds, the tendency to form saprophytic types connect this family with the other representatives of this evolutionary group.

Summary: In the anomalous evolutionary group the extremists among the Monocotyledons, with regard to the morphological structure of the body as well as to the mode of life, have been grouped together. They are types which are usually referred to evolutionarily different families. Some types represent really taxonomic puzzles. The common character of all the families of this group is the tendency to form unusual shapes, though in some there are also very sober types. Some species are very rare, and are found only in small numbers in the herbaria, and thus they have mostly been imperfectly studied. Thus their final placing is not yet possible. It is also a quesiton whether the affinity of these types is not merely apparent. It is possible that there are here types of different evolutionary groups modified by the saprophytic mode of life. Yet they have developed some common characters which occur rarely in other families. Thus the types with inferior ovaries, the *Apostasiaceae, Burmanniaccae, Thismiaceae, Corsiaceae,* and *Orchidaceae,* form certainly a natural group. They have many characters in common, such as small seeds, reduction of some flower parts, perianth not differentiated into calyx and corolla, embryo not differentiated, tendency to saprophytism, etc.

The families with a superior ovary may already be evolutionary alien. It is, however, difficult to find a family to which they would approach more by their whole evolutionary trend than to this group. The often huge variation in the structure of their flower and their very unusual shapes and properties might indicate that they originated as lateral, unsuccessful types of this evolutionary group. Thus the whole group may have differentiated by a similar evolutionary trend as e. g. the *Helobiae,* i. e. from apocarpous superior to syncarpous inferior gynoecia. Both groups might be also somewhat related. The *Orchidaceae* have e. g. in common with the *Hydrocharitaceae* the turning of the flower pedicels. This is, however, a very extreme character, which though it may appear in different evolutionary groups, yet may also indicate common ancestors. Another character which they have in common with this group is the occasional occurrence of dicotyle leaves in the *Orchidaceae.* The *Triuridaceae* also somewhat approach the hydrophile group by their evolutionary trend. But these are slight relations and need not signify any close affinity of these groups. The tepaloid group with undifferentiated perianth seems to be far closer.

Remarks to the Relationships of the Taxons.

The conception of a phasic origin of the plants must be shown in the diagrams representing the relationships of the taxons. Most often these relations are represented by a tree of life. This is a very attractive way, but it seems that it leads to incorrect views of the real roads of phylogenesis. Thougt one starts from the correct assumption that they originate from each other, yet the fact is not expressed that the lower taxons originate within the higher taxons. Most of the evolutionary groups show a fraternal affinity and not a genealogically progressive one. One taxon can give rise almost simultaneously to many lower taxons. The assumption that the evolutionary vigour maintains itself constantly at the same height and forms periodically equally ranking taxons seems not to be confirmed by the phenomena which we observe in nature. The paleobotanic and phytogeographic data, on the contrary, witness to the possibility of an approximately simultaneous origin of equally ranking taxons as e. g. families. The differentiation of most families took probably place simultaneously. The plastic stock disintegrated into a number of centres which represent the stock of the different evolutionary groups. In these centres new, weaker centres became differentiated, representing the stocks for the individual families. In these centres with a weaker evolutionary vigour the genera became differentiated, and in these still weaker centres the species. This differentiation in consequence of the similar material composition could proceed similarly in the different centres. The agreeing morphological structure thus need not signify a close affinity, but may often be due only to a similar evolutionary predisposition. The differentiation of each plastic centre from the point of view of the evolutionary vigour took place in the direction towards greater specialisation, but with progressive decline of the evolutionary vigour. The disintegration of the plastic stock and the differentiation of always lower taxons cannot therefore be represented symbolically by the tree of life. The tree of life represents the process of growth, but not of evolution. In growth it comes mostly only to quantitative changes, in evolution on the contrary to qualitative ones. Differentiation as a qualitative process thus cannot be schematised by the growth of a tree spreading into smaller and smaller branches. The changes taking place here are qualitatively different. The qualitative differences between the families, genera and species cannot be represented only by branches of different thickness. Evolution can best be seen from the evolutionary processes which take place e. g. in the oosfera or in the meristems. Here also from the original undifferentiated cells there differentiate by predisposition in certain layers quickly or gradually tissues and organs. The different tissues represent also a different differentiation, and the finished tissues cannot mostly be directly compared. The phylogenesis of the plant is far better represented by the schematised formation of the oosfera. The decline of the evolutionary vigour conditions the origin of lower and lower taxons within the original evolutionary plasticity. Within this schematised cell there occurs thus a more and more defined evolutionary differentiation.

An evolution of this kind is best rendered by ellipses or circles representing the evolutionary vigour of each taxon, where the lower taxons differentiate within the higher taxons. The taxons in which it comes to a greater variability of the characters can be represented by ellipses and, for taxons of a homogeneous evolution, by circles. The whole plastic stock of the Monocotyledons disintegrated probably at the very beginning into a number of evolutionary groups corresponding taxonomically to orders. These groups developed independently and each differentiated into a number of families.

As the aim of this book is to follow the macro-evolutionary evolution, only the conception of the disintegration of the Monocotyledons

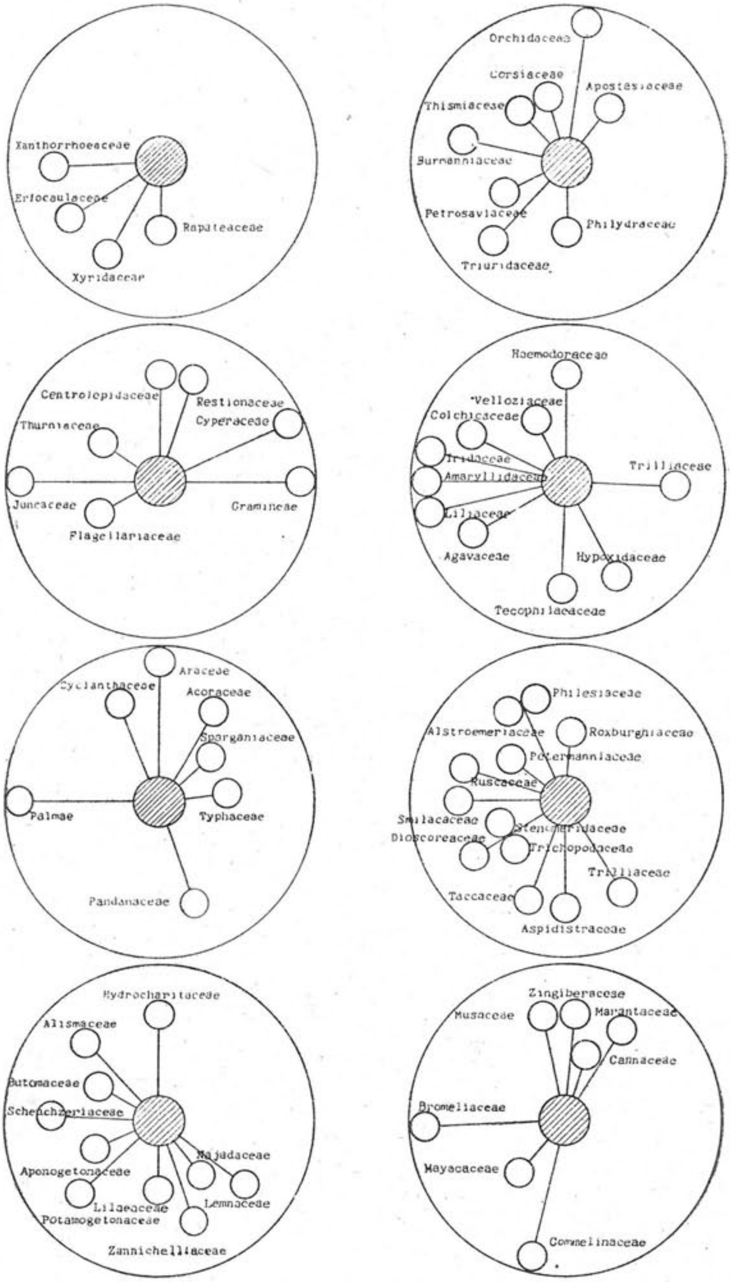


Fig. 2. — Representation of the evolutionary centres in the individual groups, and their disintegration into families. The lined inner circle indicates the plastic centre, the small circles the areas of the individual families, the straight lines connecting the plastic centre with the families the size of the evolutionary vigour of the families. The large circle delimits the individual evolutionary groups.

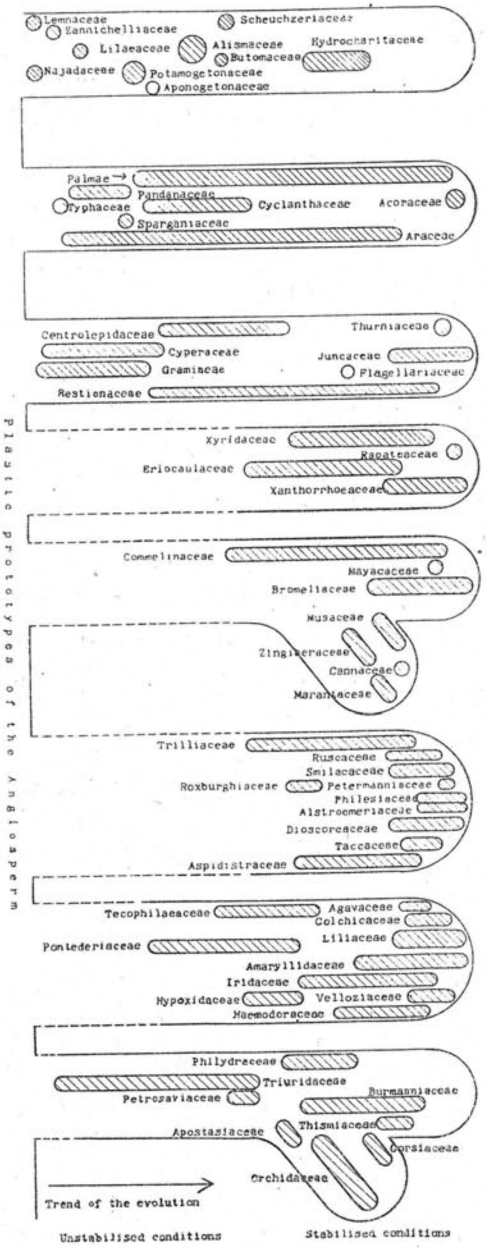


Fig. 3. — Representation of the parallel evolution of the Monocotyledons. The tongues represent the evolution of the individual evolutionary groups. The ellipses and circles within the tongues represent the position of the families according to their evolutionary valence. Evolution proceeded from the plastic centre of the Monocotyledons from the left via the apocarpous types to the predisposed syncarpous, trimerous and pentacyclic types placed at the end of the tongues on the right.

into orders and of these into families is given. Macro- and micro-evolution are often governed by different evolutionary principles, and this will be dealt with in a second part.

The present families of the Monocotyledons can be arranged into eight evolutionary groups. Each of these groups differentiated into a number of families. The evolutionary groups are the centres around which the families differentiated. The mutual relationship of the groups is thus mostly only via the plastic centre. Nor does there seem to be a direct connection between one family and another. The families represent a certain evolutionary stage and are not directly connected with each other. The similarity of the individual representatives of the different families arises mostly only by convergent evolution, and thus expresses only an apparent affinity.

In order to schematise these conditions a somewhat modified representation of the relationships was used. The plastic centre of each taxon is shown by a central lined circle; the individual lower taxons by a small circle. The plastic centre together with the lower taxons lies within a large circle which indicates the evolutionary vigour of the whole group. The individual families are connected by lines mostly only via the middle circle of the plastic centre of the group. In a similar way also the families differentiate and disintegrate into genera, and these in their turn disintegrate into species. Taxons, of which it seems that they originated directly by the splitting of taxons into two equivalent taxons, have their connection with the centre indicated only by a straight line. This we find e. g. in the *Stenomeridaceae* and *Philesiaceae,* or *Diosconaceae, Trichopodaceae* and *Roxburghiaceae.* The distances of the origins of the straight lines from the plastic centre indicate the estimated evolutionary modification of the families, and the lengths of the straight lines the size of the families.

The second diagram represents the parallel evolution of the individual evolutionary groups. Each group differentiates in a similar way. As there are so many possibilities, the differentiation never results in identity and only rarely in a great resemblance. Mostly the more distant the affinity of the taxons the less they resemble each other. Striking differences will then occur in the details. It seems that the evolution of all types begins with monocarpellate or apocarpous ovaries with undefined conditions in all flower organs. Evolution proceeds towards the stabilisation of all the flower organs at definite numbers. In the Monocotyledons the terminal evolutionary stage seems to be a trimerous, pentacyclic flower with syncarpic ovary. The evolution of the groups is represented so that the monocarpous or apocarpous families as the most primitive ones occupy the middle position in the families with unstable conditions represented mostly by ellipses. These have a great variability of the basic characters. The climax families are placed at the end of the evolutionary groups. Families with irregularly crippled flowers are shown as deviating lines, which, however, did not reach the climax.

Diagrams have always the drawback that they are considerably simplified. The diagrams figured here of the relationships are only attempts to illustrate the evolutionary processes. In reality these processes are always very intricate, and cannot be rendered perfectly by a simple diagram. A three-dimensional representation, which would be more appropriate, is very difficult, but also by simple diagrams it is possible to show the main principles of the evolutionary processes and the relations of the individual taxons.

Survey of the Monocotyledons.

As a survey I give also a list of the orders and families of the Monocotyledons. The evolutionary groups correspond to the orders and are designated after the most perfectly differentiated family of the group. According to the conceptions given above the Monocotyledons are divided as follows:

Order 1. *Hydrocharitales.*
  Families: *Lilaeaceae, Najadaceae, Zannichelliaceae, Lemnaceae, Potamogetonaceae* (incl. *Ruppiaceae, Zosteraceae, Possidoniaceae*), *Aponogetonaceae, Scheuchzeriaceae* (incl. *Juncaginaceae*), *Butomaceae, Alismaceae, Hydrocharitaceae.*

Order 2. *Arecales.*
  Families: *Araceae, Acoraceae, Pandanaceae, Sparganiaceae, Typhaceae, Cyclanthaceae, Palmae.*

Order 3. *Juncales.*
  Families: *Gramineae, Cyperaceae, Restionaceae, Centrolepidaceae, Thurniaceae, Flagellariaceae, Juncaceae.*

Order 4. *Xanthorroeales.*
  Families: *Eriocaulaceae, Xyridaceae, Rapateaceae, Xanthorrhoeaceae.*

Order 5. *Bromeliales.*
  Families: *Commelinaceae, Mayacaceae, Musaceae, Zingiberaceae, Cannaceae, Marantaceae, Bromeliaceae.*

Order 6. *Dioscoreales.*
  Families: *Trilliaceae, Aspidistraceae, Taccaceae, Ruscaceae, Smilacaceae, Alstroemeriaceae, Philesiaceae, Stenomeridaceae, Trichopodaceae, Roxburghiaceae, Petermanniaceae, Dioscoreaceae.*

Order 7. *Liliales.*
  Families: *Pontederiaceae, Hypoxidaceae, Velloziaceae, Haemodoraceae, Tecophilaeaceae, Agavaceae, Colchicaceae, Iridaceae, Amaryllidaceae, Liliaceae.*

Order 8. *Orchidales.*
  Families: *Triuridaceae, Petrosaviaceae, Philydraceae, Apostasiaceae, Burmanniaceae, Thismiaceae, Corsiaceae, Orchidaceae.*

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