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Studie k otázce o původu a fylogenetickém vývoji krytosemenných rostlin

PŘEDMLUVA.

Theoretická studie, kterou předkládám v následující anglicky sepsané stati, představuje vlastně druhou část k mé obdobně zaměřené studii z roku 1950, kde jsem vyložil své názory zaměřené hlediskem paleontologickým na vývoj a taksonomii rostlinné říše až po její nejmladší („nejmodernější“) a morfologicky i anatomicky nejkomplikovanější příbuzenský okruh, to jest rostliny krytosemenné. Učinil jsem tak tehdy úmyslně, neboť k posouzení této nejmladší skupiny nám zdaleka naše paleontologické znalosti nestačí do té míry, jako na příklad u pteridofyt nebo gymnospermů. A tu bylo třeba předem prostudovati a uvážiti celou řadu poznatků a názorů na morfologickou a anatomickou úpravu dodnes žijících zástupců. Povaha paleontologických nálezů z tohoto příbuzenského kruhu jest totiž na rozdíl od nálezů fosilních pteridofyt a gymnospermů shodou fosilizačních okolností poněkud jiného rázu: nejčastěji pouhé otisky listů. Květy, plody a semena, které by nám do těchto otázek mohly vnést více jasna a spolehlivosti, jsou daleko vzácnější. A tak paleontologie nám tu dává spíše odpovědi na různé otázky týkající se geografického rozšíření našich nálezů, než jejich povahy morfologické a anatomické. Paleontologické nálezy nám v tomto případě skýtají ponejvíce oporu tam, kde jest třeba se vyvarovati chyb při odvozování jedné skupiny příbuzenské od druhé, a to v tom smyslu, abychom správně vystihli jejich vzájemný poměr odvozenosti a neodvozovali okruhy geologicky prokazatelně staré od příbuzenstev relativně příliš mladých. Také nám mohou poskytnouti objektivnější obraz o nejstarších výskytech zástupců z této skupiny, jejich geografickém rozšíření v minulosti a tím i jasnější pohled na celou otázku jejich vzniku a rozvoje.

Při všech úvahách dal jsem se stejně jako ve své studii z r. 1950 i zde vésti dvěma základními myšlenkami, které čím dále tím více ovládají mysl botaniků zabývajících se poslední dobou podobnými otázkami a které jako červená nit se zračí v průběhu celého rostlinného vývoje: přizpůsobování se k životu za podmínek vysloveně terestrických a s tím souvisící postupná

kondensace a redukce různých orgánů. Jest třeba ovšem zde mít stále též na paměti i druhotné, zpětné přizpůsobování rostlin k jejich původnějším podmínkám životním, to jest zpětně k prostředí silně vlhkému nebo vodnímu.

Snažil jsem se také pokud možná oceňovati rovnoměrně různé soubory znaků anatomických a morfologických. A tu v ohledu anatomie přicházím k názoru, že dosud poměrně málo váhy bylo přikládáno zejména úpravě sítkovic v lýku ve srovnání s důrazem, jaký jest běžně přikládán stavbě dřeva.

U listů i sporofylů krytosemenných rostlin předpokládám vesměs makrofylní povahu, připouštím ale, že sporofyly mohly vznikat z telomoidních útvarů, které nemusely stejnou měrou mít čepel vyvinutou jako normální listy asimilační. Odchylný ráz angiospermických listů od typu kapradinovitého nebo cykasovitého vysvětlují zastavením původního směru vývoje na jistých neotenických stadiích vlivem vysloveně terestrických podmínek a nastoupením zcela odchylného vývojového směru. Proto snad také neznáme přechodných zjevů mezi listy rázu pteridofytního a cykasovitého a mezi listy rázu angiospermického.

Pokud se jedná o květní morfologii, tu docházím k závěru, že angiospermické květy jsou vesměs povahy euanthiové, ale že rozdíly zde mohou být předpokládány ve způsobu vzniku korunních resp. okvětních lístků. Na rozdíl od pravých kališních lístků, které vždy vznikly redukcí asimilačních listů, mohly korunní nebo okvětní plátky vzniknout buď sterilisací a kladodifikací původně fertálních sporofylů (tyčinek) anebo z redukovanych asimilačních listů („stegofyly“). Bude proto podle toho třeba rozlišovat dvojí druh květů (zavádím pro ně název květů homogenních pro první a heterogenních pro druhý případ), což se nesporně musí také odrazit v soustavě angiospermů. Mluvit o stachyosporii u angiospermů, jejichž listy i sporofyly považují za útvary vesměs makrofylní, pokládám za nemožné; veškeré angiospermické květy jsou jistě povahy fylosporní.

Podle různých paleontologických nálezů kladu vznik angiospermů někam do mladšího paleozoika, kde se odštěpily jako poměrně omezená a extrémně terestrická větev (snad pod vlivem hercynského vrásnění a tehdejšího klimatického rozkolísání) od velmi různotvárného okruhu pteridofytního *Profilicineae*, které daly vznik též pravým kapradinám a rostlinám cykasovitým, a to zřejmě od nějakého okruhu, který neměl ještě náležitě vyvinuté dvojtečkované tracheidy, tedy paralelně (a možná i dříve) ke skupině *Gnetineae*. Ve starším mesozoiku nutně musíme předpokládati již existenci velmi různých řádů a čeledí i když se ještě někde v uloženinách jejich zbytky hromadně neobjevují, neboť v pozdní fázi spodní křídly jest celý tento okruh již roztržštěn ve všechny podstatné dnešní taksonomické hlavní jednotky. Podle povahy a geografického rozšíření různých květů v pozdním paleozoiku a v mesozoiku i podle způsobu fosilizačního známých nálezů musíme předpokládati, že vývojové kořeny angiospermů tkví v květeně permokarbonské euramericko-kathaysijského pásma (tropy-subtropy) a to v oblastech tehdejších vyvrásněných pohoří. Není však žádného podkladu, proč klást místo jejich vzniku právě do oblasti indomalajsko-pacifické, jak se tak často s oblibou poslední dobou předpokládá. Jejich

vývoj šel z počátku asi značně pomalým tempem, neboť od doby, co známe první nálezy angiospermídního pylu (spodní karbon), uplynula velmi dlouhá doba, než se objevily některé jejich vzácné zbytky makroskopické (listy, dřeva; rhät, lias). Soudě nejen podle časového sledu nálezů, ale i podle morfologických a anatomických vlastností dosud žijících typů soudím, že hlavní vývoj měl tři základní fáze, jež zanechaly zejména stopy v organizaci květů. Mluvím proto o I., II. a III. vývojovém stupni. Tu celkem souhlasím s Deylovým pojetím jejich rozvoje. Různé typy pak nestejněměrně na některém z těchto stupňů zaostávaly a po případě odštěpovaly i postranní vývojové větve, jakési deriváty, přizpůsobené po případě i na zcela speciální životní prostředí (sympetální, amentiferní, vodní, hmyzožravé, saprofytické, parazitické a pod.). Kdy a jak se takové linie odštěpovaly nebo ve vývoji zaostávaly, dá se odhadnouti do jisté míry z jejich anatomické povahy, rázu květů, velmi často i z povahy pylu.

S ohledem na tyto i jiné okolnosti projednávám blíže v následujících anglicky sepsaných statích předpokládám, že již samotný permokarbonský základ, který později dospěl k angiospermii, i když byl jistě značně úzký, jistě byl již roztržštěn ve více od sebe se různících typů. Proto nejsem toho názoru, že by bylo možné sestaviti veškeré angiospermy v jeden jediný společný rodokmen. Taksonomicky zde vymezují proto celkem 6 vývojových okruhů, u kterých snad se dají předpokládati květy heterogenní povahy (*Trochodendrineae*, *Eucommiocercidiphyllineae*, *Amentiferineae*, *Urticoplatanineae*, *Centrospermíneae* a *Geraniorhamnineae*), a 11 okruhů, u kterých snad můžeme předpokládati s jistou pravděpodobností květy rázu homogenního (*Polycarpiceae*, *Dilleniineae*, *Canellineae*, *Hamamelidíneae*, *Rhoeadíneae*, *Cruciferineae*, *Parietaleae*, *Saxifragorósineae*, *Columniferotricocceae*, *Guttiferomyrtineae* a *Umbelliferocelastrineae*; vedle toho též dva prastaré sympetální deriváty: *Sapotoprimulíneae* a *Thymelaeoproteíneae*). Rostliny monokotylní se nám v této soustavě objevují jako speciální derivát od okruhu polycarpického a samy představují nejméně asi 6 samostatných vývojových linií. Nemyslím však, že by tu bylo možné mluvit o polyfyletičnosti v tom smyslu, jak poslední dobou mnozí prohlašují (Emberger, Lam, Kuzněcov, Greguss a j.), totiž že by kořeny jejich vzniku tkvěly ve dvou nebo třech, po případě i více naprosto různých vývojových větvích pteridofytních. Mnohem pravděpodobněji se zde jedná jen o rozpad určitého úzkého příbuzenstva rázu skupiny *Profilicíneae* ještě před dosažením angiospermie.

S ohledem na naše omezené tiskové možnosti musel jsem i anglickou stať osvětlující blíže tyto názory proti původnímu záměru podstatně stručněji upravit a upustit od výkladů mnohých obecně známých zjevů. Laskavý čtenář může si však bližší poučení o takových otázkách nalézt v literatuře na konci tohoto spisu citované. Považuji pak ke konci za milou povinnost poděkovati za anglickou úpravu celé hlavní stati panu Dr. Vladimíru Jindrovi, který se tohoto ne právě snadného úkolu s nevšední ochotou a úspěšně ujal, a pak mému příteli univ. prof. Dr. F. A. Novákovi za laskavé předběžné prohlédnutí k tisku připravovaného rukopisu.

Ф. НЕМЕЙЦ:

Изыскания по вопросу происхождения и филогенетического развития покрытосеменных растений

ПРЕДИСЛОВИЕ.

Теоретические изыскания, которые я привожу в нижеследующей статье, написанной на английском языке, представляют, в сущности, вторую часть моей работы с той же тематикой, написанной в 1950 г., в которой я изложил свои взгляды, с точки зрения палеонтолога, на развитие и таксономию растительного царства, исключая его самый молодой («наиновейший») период и морфологически и анатомически наиболее сложный родственный округ покрытосеменных растений. Это я сделал умышленно, т. к. для оценки этой наиболее молодой группы нам далеко не хватает наших палеонтологических знаний, как например у птеридофитов или гимносперм. Здесь необходимо было заранее изучить и извесить целый ряд гипотез и взглядов на морфологическое и анатомическое строение до настоящего времени живущих представителей. Характер палеонтологических находжений из этого родственного округа в отличие от находжений фосильных птеридофитов и гимносперм сходством обстоятельств частично иного характера: чаще всего лишь отпечатки листов. Цветы, плоды и семена, которые бы могли внести известный свет в эти вопросы и дать известную уверенность, встречаются исключительно редко. Итак палеонтология дает нам здесь ответы вернее на различные вопросы, касающиеся географического распространения наших находжений, чем о их морфологическом и анатомическом характере. Палеонтологические находжения в данном случае дают нам известную поддержку там, где необходимо избежать ошибок во время установления одной группы родственной по отношению к другой, а именно в том смысле, чтобы мы могли правильно показать их взаимное отношение и не определяли круги геологически доказанные старые от родственников им относительно слишком молодых. Также, более объективный образ о наиболее старых местонаходжений представителей этой группы нам могут дать их географическое распространение в прошлом, и этим и более ясный взгляд на весь вопрос возникновения и развития.

Во время всех моих суждений, точно также, как и в работе от 1950 г. мной руководили две основные мысли, которые чем дальше, тем больше захватывают ботаников, посвятивших себя разъяснению этих вопросов, и которые красной нитью проходят на протяжении всего развития растительности: приспособливание к жизни в условиях явно терестрических и с этим связанная постепенная конденсация и редукция различных органов. Здесь однако необходимо иметь всегда в виду и вторичное обратное приспособливание растений к их более первоначальному жизненному окружению, т. е. возвращение в значительно сырую или водную обстановку.

Кроме того я старался по мере сил и возможностей оценивать равномерно различные скопления знаков, как анатомических, так и морфоло-

гических. Тут, принимая во внимание анатомию, я прихожу к заключению, что до настоящего времени сравнительно мало уделялось внимания в особенности флоэмы в сравнении с тем значением, которое приписывалось структуре ксилемы.

У листьев и спорофил покрытосеменных растений я предполагаю в большинстве случаев макрофильный характер, однако я допускаю, что спорофилы могли возникать также из теломоидных формаций, у которых не должны были быть развиты пластинки, как у нормального ассимиляционного листа. Отличимый характер ангиоспермических листьев от типа папоротникового или цикасного я объясняю остановкой первоначального направления развития в различных неотенических стадиях влиянием явно террестрических условий их совершенно отличительного направления развития. Поэтому мы возможно и не знаем переходных явлений между листьями птеридофитного и цикасного характера и между листьями ангиоспермидного характера.

Что касается цветной морфологии, я прихожу к заключению, что ангиоспермические цветы в большинстве случаев эуантионного характера, и, что различие здесь можно предполагать в способе возникновения венчиковых или же околоцветниковых листьев. В отличие от действительных чашечкообразных листьев, которые всегда возникали благодаря редукции ассимиляционных листьев, венчиковые или околоцветниковые могли возникнуть или же путем стерилизации и кладодификации первоначально фертильных спорофил (тычинок) или из редуцированных ассимиляционных листьев («стегофилы»). Поэтому необходимо различать два вида цветов (я ввожу для первых — название гомогенных а для вторых гетерогенных), что естественно должно также отразиться в системе ангиосперм. Говорить о стахиоспории у ангиосперм, листья которых, также как и спорофилы я принимаю за формации макрофильные, я считаю не возможным; все ангиоспермические цветы конечно филоспорного характера.

На основании различных палеонтологических находений я отношу возникновение ангиосперм к младшему палеозою, в котором они отделились как сравнительно ограниченная и террестрическая ветка (возможно, что под влиянием герцынского складкообразования и под влиянием тогдашних климатических условий), от весьма разнообразного округа птеридофитного *Profilicineae*, которые дали возникновение действительным папоротникам и цикасным растениям, а именно, вернее всего от какого нибудь округа, у которого еще как следует не развиты двучленные трахеиды, т. е. параллельно (а может быть и раньше) к группе *Gnetineae*. В более старшем мезозою мы должны предположить наличие весьма различных рядов и семейств, хотя пока что еще нигде в отложениях их остатки массово не обнаружились, т. к. в позднейших фазах нижнего мела весь этот округ разбит на все основные современные главные таксономические единицы. По характеру и географическому распространению различных флор в позднем палеозою и в мезозою и по способу фосильных известных находений мы должны предполагать, что корни развития ангиосперм заключаются в флоре пермокарбонного еурамерическо-катаисийского пояса (тропики, субтропики) а именно, в областях тогдашних погорий. Однако нет никаких оснований, относить место их

возникновения именно в область индомалайско-пацифистскую, как это в последнее время очень часто предполагают. Их развитие происходило в начале весьма медленными темпами, т. к. от времени, от которого нам известны первые находения ангиоспермидной пыльцы (нижний карбон), прошел очень длинный период времени, пока появились некоторые их редкие макроскопические остатки (листья, дерево; рет, лиас). На основании временной последовательности, а также и по морфологическим и анатомическим качествам до сих пор живущих типов я сужу, что их главное развитие имело три основных фазы, которые оставили следы главным образом в организации цветов. На основании этого я говорю о I, II, и III ступенях развития. Здесь я всецело согласен с пониманием их развития М. Девилом. Различные типы неравномерно в какой то из этих ступеней оставали или же отделялись в ветви развития, в виде каких-то дериватов, приспособленных в случае надобности к совершенно особым специфическим условиям (симпетальному, аментиферному, водному, насекомопожирающие, сапрофитические, паразитические и т. д.). Когда и как подобные линии отделялись или отставали с развитием, возможно предугадать до известной степени по их анатомическому характеру, виду цветка, весьма часто также и по характеру пыльцы.

Принимая во внимание эти и другие обстоятельства, приведенные в нижеследующей статье написанной на английском языке, я предполагаю, что уже самостоятельный пермокарбонный базис, который позднее достиг ангиоспермии, несмотря на то, что он был очень узкий, наверное был разделен на большое количество разнящихся между собой типов.

Поэтому я не придерживаюсь мнения, что возможно все ангиоспермы составить в одно общее родословное дерево. Таксономически я здесь выделяю поэтому всего 6 округов развития, в которых возможно предполагать цветы гетерогенного характера (*Trochodendrineae*, *Eucomio-cercidiphyllineae*, *Amentiferineae*, *Urtico-platanineae*, *Centrospermineae* и *Geranio-rhamnineae*), и 11 округов, в которых возможно предполагать с большим вероятием цветы гомогенного характера (*Polycarpiceae*, *Dileniineae*, *Canellineae*, *Hamamelidineae*, *Rhoeadineae*, *Cruciferineae*, *Parietaleae*, *Saxifrago-rosineae*, *Columnifero-tricocceae*, *Guttifero-myrtineae* и *Umbelifero-celastrineae*; наряду с этим два исключительно старых симпетальных деривата *Sapoto-primulineae* и *Thymelaeo-proteineae*). Растения монокотыльные в этой системе проявляются в виде специального деривата из округа поликарпического и сами представляют не меньше чем 6 почти самостоятельных линий развития. Однако я не думаю, что можно было бы говорить о полифилетичности в том смысле, в котором в последнее время ее понимают (Эмбергер, Лам, Кузнецов, Грегусс и др.), а именно, что корни возникновения в двух или трех, а может быть и большем количестве совершенно различных птеридофитных веток развития. Гораздо правдоподобнее, что здесь мы имеем дело с распадом известного узкого родства характера группы *Profilicineae* еще перед достижением ангиоспермии.

Принимая во внимание ограниченные печатные возможности мне пришлось также и английскую статью, подробнее объясняющую эти взгляды переработать и упростить от изложения многих известных явле-

ний. Однако читатель может найти ответы на эти вопросы в литературе, которая приведена в конце моей работы. В конце концов считаю своей обязанностью поблагодарить Др. Владимира Йиндру за переводъ моей работы до английского языка, который с исключительным усердием исполнил эту сложную и непривычную работу, а также профессора университета Др. Ф. А. Новака за просмотр рукописи.

F. NĚMEJC:

On the Problem of the Origin and Phylogenetic Development of the Angiosperms

I. Introduction.

Today, the Angiosperms indisputably represent the most widely spread plant type. Fossil evidence clearly shows that their phenomenal rise to a place of dominance goes as far back as the middle phase of the Cretaceous. As a plant type still living in great numbers, they are, therefore, thrown open to our observation, decidedly more so than any lower organized plant groups from which only relicts have come down to us, or which became entirely extinct long ago. In spite of this, there is a great number of problems, or at least certain impossibility of taking any definite statements as to their origin, and many features in their morphology are still wrapped in a shroud of mystery.

During the last two decades there have arisen many doubts about the so far suggested morphological interpretations of various angiosperm organs, particularly the floral organs, which must be correctly understood, should the conclusions with reference to the whole phylogeny and the system of this most progressive plant group be of any scientific value. It is the discovery of a whole series of extremely primitive vascular plant types dating from the Silurian and Devonian (the group *Psilophytineae* and some primitive pteridophytic plants most closely related to it) which has shown so many classical morphological theories (together with the anaphyte theory dealing with the morphological basis itself of the body of the higher organized plants) in a very artificial light. There are several reasons for it, resting, to a great extent, on the kind of our palaeontological knowledge of this group.

First of all, in spite of an enormous abundance of fossil remains, our palaeontological knowledge of the basic principles of the *Angiospermae* is the poorest, when compared with what is known about all the other groups of vascular plants. Their fossil record is mostly represented by leaf imprints; disproportionately more rare are fossilized fruits and seeds, whereas flowers or their parts stand entirely in the background. Because of an amazing possibility of convergences, mere leaves are, of course, the least suitable material for considering phylogenetic evolution and mutual relationship. They may prove a good criterion in palaeogeographic researches, especially if due attention is paid to considerations resulting from a better

knowledge of fruits as well as seeds and from modern palynological discoveries. Here, too, the greatest difficulty lies in that the Angiosperms appear relatively late, that is, as late as the middle phase of the Cretaceous, when all the families, which have persisted up to now, seem to have been entirely fixed. Angiosperm fossil evidence from older periods is so scanty that whatever we possess does not give us any idea as to their relation to the *Gymnospermae* or *Pteridophyta*. The second strange fact is that, despite an enormous variety in forms, this group shows a more than amazing homogeneity in certain fundamental features (axillary stem branching, structure and arrangement of vascular bundles, fundamental features in pollen-grains as well as the mode of their germination, double fertilization, mode of production of endosperm) which is in support of the so far current opinion as to a rather monophyletic character of its origin. On the other hand, an enormous diversity prevailing in various minute characteristics is a source of innumerable combinations and permutations in which we get, as it were, drowned and easily lose a general survey. The third difficulty lies in the present-day general conception of the morphology of these plants; according to it the Angiosperms themselves were, until not long ago, the only subject of researches and no due attention was paid to an appropriate interpretation of the structure of their bodies, based on the knowledge of the primitive vascular plant types we know of. Only recently the latter method has been taken up, and this has given rise to many most different and contradictory ideas.

The aim of this paper is not reveal any fundamental new facts in this maze of problems, but first to evaluate all hitherto acquired knowledges, and then to arrive at certain basic principles of the origin and development of the Angiosperms which would agree with their palaeontological record and serve as a basis for establishing some definite outline of their system.

II. Origin of the Angiosperms and Their Development in the Cretaceous.

In solving this problem we must, first of all, confess that a great many errors which have slipped in our views are due to a rather imperfect picture supplied by various fossil records from the history of the plant kingdom as a whole. The basic idea that morphologically and anatomically more complex forms are to be derived from more primitive, or, stated in better terms, from simpler types is, to a great extent, justified. Only some facts, based on phylogenetic researches that have been carried on for about the last three decades have to be added: Ancestors of such advanced types are not to be looked for among primitive, although appropriately specialized, groups, but among such Palaeozoic types in which conditions of both fructification and anatomy were far from being so definitely fixed (e. g. with reference to the *Cycadales*, not among highly specialized pteridospermous orders *Lyginopteridales* or *Medullosales*, as is often done, but more probably in the neighbourhood of the orders *Dicksonites*, *Eremopteris*, *Pteridozamites* a. o.). To the author's opinion the chief error lies in the fact that such considerations are still too rectilinearly established on

tracing the main plant groups (the *Psilophytineae* in the Devonian, the *Pteridophyta* and *Pteridospermae* in the late Palaeozoic, more advanced *Gymnospermae* in the Mesozoic) without paying due attention to palaeobiologic as well as palaeoecologic conditions and especially to the whole dynamics of events actually conditioning the entire phylogenetic development of vascular plants, that is, more and more ingenious adaptation to life on dry land exposed only to a greater or a lesser amount of periodical precipitations. Here we must admit that the most fossil floras we know are rather strongly hygrophilous; it is only at such places as marshy lowland areas, sea-coast deltas, large inland coal-forming sedimentary basins that fossilization is duly ensured in great amounts, whereas in typically dry-land, hilly, or even mountainous areas this process could have taken place only on a very small scale. The sediments of hilly or mountainous regions dating from considerably old geological times had not at all the chance of being preserved due to their smaller extent and, moreover, because in the course of time they were to a greater degree subject to being washed off. It is only since the Cretaceous and chiefly the Tertiary that larger or smaller deposits of this kind begin to occur. It must be therefore above all realized that truly terrestrial floras belonging to older geological phases are practically unknown. In spite of this, here and there, some elements of these floras have come down to us (of course, in a very poor state, e. g. pieces of silicified stems, leaf petioles, pieces of wood, a. o.) if carried away by water streams from their original sites and deposited in large sedimentary basins. In that case they often show far more advanced features than do the autochthonously fossilized forms predominantly occurring with them. This circumstance has to be taken into account in the first place, when such a strictly terrestrial element, as are just the Angiosperms, is concerned.

Finally, there is still another circumstance which in considerations of this kind is usually rather spontaneously overlooked. Most phylogenetic considerations are based on autochthonal fossil record yielded by the already mentioned sedimentary areas, because, upon the whole, we do not know much more from older periods. A more detailed examination of these elements, however, shows that most of them became adapted to such moist conditions secondarily. When tracing the morphology and anatomy of various autochthonal fossils we can easily see that the real primary hygrophilous types (it cannot be denied that the aquatic environment was actually the cradle of all the vascular plants) were since Silurian and Devonian times rapidly decreasing in numbers, whereas type secondarily adapted to such environments became more frequent. We may ask what is the cause of it. No due attention is being paid to this problem either, although the answer is very simple. The rate of the evolutionary process in the plant kingdom depended largely on the formation of the relief of the continents. In certain periods the continents were subjected to violent mountain-forming processes which were always accompanied by sudden fluctuations in climatic conditions. All this, of course, affected, or at least accelerated, the development of, and apparently gave rise to, a whole series of new strictly terrestrial types which under suitable circumstances became secondarily adapted to moist conditions. This process was steadily

increasing in intensity in proportion to the progress of denudation of mountainous and hilly areas, and caused these types to descend to lower places, sometimes even to areas of moist sedimentary basins. An excellent example for this is the Palaeozoic group of *Cordaites* and *Walchia* whose ancestors can hardly be looked for among the old hygrophilous flora of the Carboniferous and Devonian sedimentary basins. Much more in common with their ancestors seem to have some allochthonous fragments and branches most frequently known as *Pityae*. The same has to be applied to the origin and development of the Meso- and Cainozoic Angiosperms. Thus the ancestors of all new plant types, appearing autochthonously in the course of geological periods, are mostly to be looked for in older, still typically terrestrial elements which under suitable circumstances descended from hilly regions to low-land areas or altogether sedimentary basins. The evolutionary process the sequence of which is: pteridophytic elements in the Devonian, pteridophytic and pteridospermous elements in the Permo-Carboniferous, more advanced gymnospermous elements in the Mesozoic, and predominantly angiospermous elements in the Cainozoic—offers therefore a picture chronologically coordinated, not with the progressive phylogenetic evolutionary tendency of the plant kingdom, but rather with the adaptations and descent of terrestrial types (which came into existence long time before) to marshy basins and lowlands, as well as with gradual dying-out of primary aquatic and hygrophilous types. Only indirectly is this process coordinated with the actual formation of new plant elements. Although not to all consequences, it is on this phenomenon that some up-to-date considerations as to the origin and spreading of the angiospermous element are based (e. g. D. I. Axelrod in the U. S. A. and V. A. Vachrameev in the U. S. S. R.). There are, therefore, quite a good many reasons for the assumption that the origin of the Angiosperms is to be looked for outside the low-land or sedimentary-basin areas.

There arises, of course, the question whether we have a sufficiently strong body of evidence in support of the view that such new plant elements do appear as a rare allochthonous admixture before they become fully developed in the shape of an autochthonous element found in sedimentary basins. Taking into consideration the whole series of fossil record from most different geologic formations, this question may be answered in the affirmative. We have come in touch with this problem when dealing with the flora of the late Palaeozoic (*Cordaites* and *Walchia*). In this period, not only some pteridospermous (*Cordaites*), but also some higher gymnospermous types descended from their higher sites, as is proved by rare records of the cycadean types going as far back as the Westphalian, as well as of the ginkgoean and coniferous types dating already from the Stephanian, although these plants do not show any appreciable development until in the Lower and even Upper Permian. The same can be stated with reference to the angiosperm remains occurring during the Upper Triassic and in the Jurassic. It is especially the recent palynological researches that have supplied large number of evidence proving this phenomenon: spores of terrestrial cryptogamous plants found already in Cambrian strata, spores quite similar to angiospermous pollen-grains discovered

already in the Lower Carboniferous (by S. N. Naumová in the Moscow coal basin) and finally numerous indisputably angiospermous pollen-grains found in deposits dating from the Liasso-Rhaetic (J. S. Simpson, G. Erdtmann, S. N. Naumová). All this makes it quite evident that the angiospermous element had been in existence on the earth, of course, much earlier outside the low-land and basin areas, before it prevailed in the course of the mid-Cretaceous also in the vegetation of the sedimentary areas. The so far known circumstances lead us to the assumption that it was arising perhaps during the late Palaeozoic, that is, under the influence of Hercynian mountain-forming processes which were accompanied by climatic unrest. The period of the Mesozoic orogenic rest in the Triassic and Jurassic ensured its development and splitting into separate evolutionary lines (families and orders) and finally, after a sufficiently long phase of denudation, ranging from the close of the Palaeozoic to the Upper Jurassic, its descent to sedimentary areas (in the late phase of the Lower Cretaceous). This is the explanation of the fact that since the very beginning (in the Barremian, Aptian and Albian) these areas yield angiospermic fossils of most different groups, as they are known today, and even sympetalous types. Nor are the Monocotyledons missing here, although they are very rare in this period; they do not become more abundant until the Senonian stage of the Upper Cretaceous.

The problem as to under which climatic conditions and in which regions this angiospermous plant element came to existence has for a long time been an open question. Much may become clear from a detailed analysis of conditions governing the geological period, into which we have placed its origin as well as its development, and perhaps, to some extent, from the analysis of certain phenomena occurring in the present-day geographical distribution of considerably primitive angiospermous elements. The investigators who for the most adopt the latter method are in favour of putting the cradle of Angiosperms into the areas of the warmer Pacific where so many strange and very primitive plant types still are to be found on many islands (e. g. the genus *Degeneria*). Today, however, we know of indisputably angiospermous remains dating already from the Upper Triassic or Lower Jurassic (or the Jurassic in general) and found in regions so distant from one another (i. e. Greenland, England, France, South Germany, Sweden, Central Asia, South Africa) that only one centre of origin would not be sufficient. This fact rather supports the opinion that the ancestors of the angiospermous plant type represented some considerably common late Palaeozoic plant type which became adequately modified for strictly terrestrial life. Accordingly, the whole problem is to be considered from the point of view of various palaeoclimatic and palaeogeographic changes taking place during the late Palaeozoic. Investigators who base on this point of view their theory as to the origin not only of the Angiosperms, but also of new plant types occurring in the post-Palaeozoic periods in general (i. e. gymnospermous types included) most often refer to the time of the geobotanical splitting of the Palaeozoic flora in the late Carboniferous and early Permian; they suggest that such new elements may have arisen in areas which in the Stephano-Permian ice period came under the influence of periodically increasing and decreasing sheets of

everlasting ice and snow, i. e. in the Angara area on the northern and in Gondwanaland on the southern hemisphere. To their opinion it is the drastic interference of climatic changes by which the formation of new progressive plant elements was called forth. Analysing impartially the Gondwana Permo-Carboniferous flora (and analogically also the Angara floras) we can easily see that, as a matter of fact, these floras comprise elements doubtlessly adapted and specialized to a rougher climate, but of no great importance for the general evolutionary progress in the Plant Kingdom, i. e. only some lateral evolutionary lines which underwent a strong specialization. These lines, however, cannot be considered as a source of further progressive descendants: they became specialized at the expense of their plasticity. Besides, really progressive elements sporadically appeared earlier, not in the colder Gondwana area, but in the then warm Euramerico-Cathaysia zone. It is just in this zone, where the flora continued to remain under the influence of a relatively warm, at some places considerably moist climate, that as early as the Westphalian we come across not only rare records of leaves quite similar in shape to those of the Mesozoic cycadaceous plants, but also *Dicranophylla* and other plants leading to coniferous or ginkgoean types. As a matter of fact, such elements appear therefore before the famous Glossopteris flora accompanying the great Stephano-Permian glaciation assumed its place of dominance. There is no direct link between the Glossopteris flora and the formation of new more progressive plant types. This flora represents only a pteridophyto-pteridospermous association adapted to the conditions of a temperate climate. This whole association becomes for the most part quite extinct by the close of the Permian and during the early phase of the older Mesozoic; only some of its rare elements penetrate into the Euramerico-Cathaysia zone, where later, due to further changes, levelling up of climatic conditions and appearance of really progressive (gymnospermous) plant elements, they die out without leaving any traces (during the Jurassic); thus nothing of them persist into the Cretaceous and the less so into the Tertiary.

It is therefore necessary to assume that progressive elements arose during the Permo-Carboniferous within the then wide Euramerico-Cathaysia zone whose climate, judging from other circumstances (sedimentation of coal) was by no means tropical, but rather slightly sub-tropical (at that time the equator may have passed through the equatorial Tethys sea, from the area of which no fossils are known so far). The only explanation lies therefore in the above mentioned assumption that such progressive new plant elements could have arisen only on mountainous ranges, uplifted at that period and giving their flora no chance of being preserved, and that, when these elements were coming into existence, the strictly terrestrial environment played a more important part than did the decrease in temperature. All this leads us to the opinion that the angiospermous element was most probably arising during the Permo-Carboniferous within the sub-tropical to temperately tropical Euramerico-Cathaysia zone, in mountainous, or hilly regions folded up by Hercynian orogenetic processes; the conditions under

which this evolution was going on were strictly terrestrial. This assumption agrees with a number of interesting results of researches concerning the present-day distribution of various angiospermous types (see, e. g. J. W. Bews [1927] and also D. J. Axelrod [1952] who starts from Bews's observations). Most progressive angiospermous types, occurring today in temperate or colder zones, still have their more primitive relatives in the sub-tropical to tropical zones. This may well be the inheritance from the ancient period of their arising.

There remains one more problem, namely, which is the period of the geographical spreading of more progressive elements from the places where their more primitive forefathers had their habitats for such a long time. It is commonly known that progressive elements which became adapted even to colder life conditions formed, in the course of ages, secondary centres of their geographical distribution. With regard to the character of the angiospermous flora in the middle phase of the Cretaceous (the Aptian, Albian, Cenomanian), it must be admitted that representatives of almost all the present-day orders and families were in existence already at that time. The fundamental splitting must therefore have taken place as early as the Triassic and Jurassic, which yield extremely scanty fossil record, i. e. during the period when thermal as well as humidity conditions (judging from the distribution of Ferns and Gymnosperms of that time) were, perhaps the ultimate arctic areas excepted, to a great extent stabilized all over the world. The tropics may have not been so hot as they are today and, on the other hand, today's temperate zones may have been warmer than they are at present. It was after the first attack of the Alpine earth-movement within the Upper Jurassic and during the Cretaceous that a more perceptible zonation seems to have been established on the earth. And this is also the time, when Angiosperms descended from their higher sites to assume a dominant position in low-land and basin terrains. It is of interest that at that time many types showed far greater plasticity than they do today (e. g. the genus *Artocarpus* embraced species able to grow in areas outside the tropics). It can also be easily seen that specifically circumpolar Arcto-Cretaceous floras comprising a number of new elements were formed as early as the mid-Cretaceous (the Cenomanian). Later these elements established themselves in the arising temperate zones where the more primitive and delicate tropical, as well as sub-tropical, elements were gradually disappearing. Convincing palaeontological evidence for these various facts is available and shows that the splitting of the angiospermous prototype into innumerable numbers of orders and families must have taken place at least in the late Triassic and early Jurassic; the formation of secondary centres of distribution of different more progressive or derived (i. e. special adaptations) elements may then be allotted to the middle, as well as late, Cretaceous and also to the older phases of the Tertiary, when climatic zones, called forth by the Alpine orogenetic processes, were arising. On the other hand, it cannot be assumed that during its last phase of development the angiospermous plant element could have given rise to fundamentally new plant types; most probably, the types which were unfit to live under altered conditions had to undergo mere adaptations, or else they had to die out.

III. Relation of the Angiosperms to Other Large Taxonomic Plant Groups (Fig. 1.).

The fundamental taxonomic relation of Angiosperms is quite evident from their general morphology and anatomy. It is indisputable that this type is a decidedly macrophyllous one, belonging as the ultimate evolutionary group to the series *Pteropsidineae-Pteridospermeae-Cycadeae-Gnetineae*. This classification excludes any relation to microphyllous (or sphenopsid) groups *Lycopodineae, Articulatineae, Psigmophyllineae* (i. e. *Tmesopsidineae*), *Cordaitineae, Ginkgoineae* and *Conifereae*, a relation, which has often been discussed and suggested for at least some Angiosperms (e. g. also the French palaeobotanist L. Emberger). As regards the arrangement of leaves, their quite specially complex venation, the presence of vessels and, in some cases, the mode of fertilization, the closest analogy can be found in the group *Gnetineae*. There are, however, certain features in which these two groups differ substantially; perhaps the most essential one is the formation of scalariform vessels. In the *Gnetineae* these vessels arise from a series of tracheides provided with bordered pits so that transverse rows of these pits get fused into continuous strips. On the other hand their origin in the *Angiospermae* is much simpler: here a fusion of scalariform tracheides takes place. The same occurs in some cases among the *Pteridophyta*, where vessels are also exceptionally formed (e. g. *Pteridium aquilinum*, some *Selaginellae*). This, however, apart from other details, points to the fact that between the *Angiospermae* and *Gnetineae* there is only a relation of convergence and that the gnetinean type split from substantially more advanced ancestors than did the Angiosperms, i. e. most probably a little later. This, too, agrees to some extent with palaeontological evidence. Macroscopic remains of the *Gnetineae* are extremely rare and palynologically their greatest distribution can be proved in the late Cretaceous and early Tertiary. Thus the *Gnetineae* appear to be a quite independent lateral evolutionary line which may perhaps be derived from some macrophyllous, considerably advanced types (perhaps already closely related to cycadaceous plants or at least to Pteridosperms with tracheides bearing bordered pits) and which, as regards its leaf arrangement, reached the same stage of condensation in the blade and veining as did the Angiosperms. Quite analogous is the case of the Mesozoic group *Caytoniales* which, in its turn, acquired the angiospermous character in the arrangement of ovaries without reaching the angiospermous nature of leaves. Angiosperms are to be derived from certainly far more archaic types and their origin is to be looked for, not among the *Gnetineae*, but in older periods where most probably, as will be discussed later, the Pteridosperms and primitive cycadaceous plants, still having scalariform tracheides, separated from considerably primitive macrophyllous pteridophytic types. All this is in accordance with what has been said about the geological period, in which the palaeogeographic, palaeoclimatic, as well as geologic, conditions (orogenesis, etc.) offered the greatest chance for the angiospermous plant type to come into existence.

IV. Remarks on Some Morphological and Anatomical Peculiarities of the Angiosperms.

1. *The macrophyllous angiospermic leaf.* — Angiospermous leaves may be compared only with the gnetalean leaves, especially in the genus *Gnetum*. They show a peculiar mode of growth after developing from the buds and exhibit a unique character of complex venation, quite different from that found in ferns as well as in pteridospermous and cycadaceous plants. It is usual for palaeontologists (H. Potonié, P. Bertrand) to consider them as a stage of a still more advanced coalescence of leaflets of the original much-divided frondose leaves, i. e. as a further stage of condensation of large fern like fronds. According to them the angiospermous leaf represents only a further, gradual and more advanced stage of development of what was achieved by pteridospermous or cycadaceous plants. The leaves of these plants, however, are very often provided with two leaf-trace bundles, whereas, according to S in n o t t and B a i l e y, the original state of angiospermous leaves is a palmately lobate leaf with three vascular bundles from which forms whose trace supply of the petiole consists of only one or many bundles are derived. Nor is, in fact, the angiospermous venation in any way linked with retiform venations of pteridospermous or cycadaceous plants, however complex they may be. For this reason we may take it for granted that this assumption as to the origin of angiospermous leaves is not correct and that their origin has to be linked up directly with some primitive types of leaf formations belonging to some Devonian or Carboniferous archaic plant of a still psilophyroid character, from which both Ferns and Pteridosperms originated. These leaf formations were apparently of phyllophorous character (see, e. g. the strange threefold branching of phyllophores in *Botryopteris trisecta* Mam. from the North-American Carboniferous). It is to be assumed not that such fronds underwent a gradual and* slow condensation under the influence of a slow adaptation to increasingly drier conditions but that, due to strictly terrestrial conditions, such phyllophorous formations became suddenly arrested in their growth on some initial stage (neotenic stage) from which the course of the further development of the blade took quite a different direction, with quite a different pattern of a much denser venation, far more appropriate for the distribution of water solutions in a dry terrestrial environment and therefore bearing no resemblance whatever to that of the original hygrophilous plants. We must, therefore, consider angiospermous leaves (or their blades) as a new formation having with the ancient macrophyllous archaic Pteridophyta only a common basis. In the arrangement of their blade we cannot therefore look for anything that would, from the evolutionary point of view, establish direct links with the arrangement of richly dissected fronds of the Ferns, Pteridosperms, or cycadaceous plants. This is why the idea of such complex fronds being gradually changed into entire angiospermous leaf blades is to be considered as too speculative. It is in fact probable that plant types which were developing from original hygrophilous prototypes at places sufficiently moist (low-land areas and coast or inland sedimentary basins with a strong water supply) may have very long preserved richly divided fronds, for the most part provided with

slowly growing phyllophores; cycadaceous plants are evidently their best adapted derivatives to dryer environment. On the contrary the plants which were spreading from their original environment to strictly terrestrial areas (they may have reached them quite passively when the mountain ranges were being formed by the folding of the earth's crust) seem to have been subjected to reduction very early on certain stages of their growth and formed their blades in quite a different way and of very much limited growth without contributing to the formation of any transitory shapes. This is the reason why we do not possess any leaf imprints which could be regarded as intermediary between these two leaf shapes. The same may probably be applied to gnetalean leaves.

2. *Holoblastic (monopodial) axillary branching*.—The origin of this phenomenon, so characteristic of some higher Gymnosperms and especially Angiosperms, has usually been interpreted very forcibly. It was considered to be a more advanced modification of dichotomous or hemiblastic branching and efforts were made to prove this hypothesis. Various recently found fossil remains, however, show more and more clearly that both these types of branching are apparently of the same old age. This view is supported especially by records of axillary branching in the devonian genus *Scougophyton* Term. and some Permo-Carboniferous *Coenopteridales* (e. g. some species of the genera *Ankyropteris* and *Botryopteris*). On the other hand, however, there are also some rare cases of dichotomous branching in Angiosperms (the Palm *Hyphaene*). This problem, too, is to be examined with regard to the splitting of the ancient flora into evolutionary branches, which, more or less preserving their hygrophilous nature, assumed a marked tendency for dichotomous branching, and evolutionary branches which, being of an adaptable character, went over to strictly terrestrial areas and predominantly adopted axillary branching (a better protection of growing points against desiccation). Some records go so far as to suggest that these conditions in many prototypes of vascular plants were rather unstable (see the above mentioned Palaeozoic genera). It is just in the above-mentioned Devonian genus *Scougophyton* as well as in the cited *Coenopteridales* that both the branching types may be found simultaneously on the same plant. All this, of course, indicates that the origin of such progressive plant types is to be looked for in substantially ancient times when plants possessing both kinds of branching were actually occurring at the same time.

3. *Dicotyledony and monocotyledony*.—Here, too, investigators differ in their opinions. All the latest researches (R. Souèges 1934, 1939, M. S. Jakovlev 1946, 1950, J. G. Serebrjakov 1952) are decidedly in favour of the view that the monocotyledonous type is a secondary one. This opinion certainly throws light on the phylogenesis of the whole monocotyledonous group which, accordingly, branched off from the common prototype, after this had been already sufficiently fixed in its angiospermous and its dicotyledonous nature. This agrees, to a considerable degree, with the fact that Monocotyledons reached their full development later than did the Dicotyledons, as can be traced palynologically during the Cretaceous and old Tertiary (i. g. the development of Palms).

4. *Relation of herbs to woody plants*.—As regards the herbs, many

recent anatomic researches (E. W. Sinnott, J. W. Bailey 1914, 1915, 1922; A. L. Tachtajyan [Tachtadžjan] 1948) have clearly revealed that continuous eustelic systems of vascular bundles, occasionally also the cambium ring, underwent complete disintegration. Accordingly, the herbaceous type has to be considered as a secondary one, which became specialized for particular life conditions. Investigation of conditions under which herbaceous elements occur most frequently always reveals conditions less favourable to the growth of woody plants (see, e. g., the relation of the Gondwana flora to our Euramerican or to the East Asiatic Cathaysia flora in the Permo-Carboniferous, or the relation of today's Arctic flora to the floras of the temperate zone, and the relation of these to sub-tropical or tropical floras). With the view to the whole system of vascular bundles a reverse process of evolution is hardly probable. So far all the records show that exceptional cases of herbaceous plants which became woody again (that is, woody plants which probably originated from herbaceous plants) always bear certain characteristics in their anatomic structure, distinguishing them clearly from the groups of primary woody plants. Today it is already beyond doubt that herbaceous plants are to be regarded as a highly specialized element of a secondary character which could hardly give rise to some quite new lines of evolution.

5. *The system of vascular bundles.*—As regards vascular bundles as a whole, the Angiosperms have certain features in common with the more advanced Gymnosperms. In all cases the systems are substantially eustelic and their xylem part, as compared with the cortex layer, is extensively developed. Quite the contrary to this has been found in Palaeozoic woody plants of the groups *Lycopodineae* or *Equisetineae*; the same, to a lesser extent, applies also to many Ferns and Pteridosperms of that time. But allochthonously deposited remains of various stems dating from the same period (i. e. indisputably parts of plants evidently terrestrial) prove that such a woody plant type having a thin layer of cortex tissues, but an extraordinarily bulky cylinder of wood, existed as early as that time, of course, in hilly or mountainous regions and most probably descended in the course of time from higher sites to spread also in low-land areas or sedimentary basins. This spreading took place proportionately to the degree of its ability to adapt itself secondarily to new conditions (e. g. in the Permo-Carboniferous the group *Cordaitineae*, most closely related to the group *Pityeae* which is known from predominantly allochthonous records of an evidently terrestrial character). The splitting of the plant kingdom into terrestrial and into originally hygrophilous plants can be clearly perceived in these phenomena.

In Angiosperms the eustely remains for the most part typically developed, but in some plants, especially in Monocotyledons (but also in some Dicotyledons, though not so frequently) a peculiar disintegration of the whole cylinder resulted in ataktostely. This phenomenon can be interpreted by no direct relation to external conditions, but only by an indirect one, because it was conditioned by a specific arrangement of leaves bearing numerous leaf-traces and by the mode of connecting these traces to the corresponding vascular bundles of the stem. Both the disintegration of the eustelic cylinder in herbs and the origin of ataktostely

in Monocotyledons show certain quite analogous reductional features, i. e. the disappearance of the cambium ring. In some cases (e. g. in the family *Araceae*) ataktostely is accompanied by an amphivasal character of vascular bundles, which seems to have some bearing on the multiplication of leaf-traces (E. C. Jeffrey 1917;—it appears also in the nodes of the stems of some representatives of the families *Umbelliferae* and *Araliaceae*). The evolution of the angiospermous vascular-bundle system passed from a typical eustely to ataktostely, and from here to ataktostely accompanied by amphivasal character of separate bundles. There are only exceptional cases where the bundles assumed the amphivasal character without the presence of ataktostely. Here again, the Monocotyledons, as compared with the Dicotyledons, appear to be a secondary element.

6. *Importance of more delicate anatomic structures of vascular bundles for the taxonomy of the Angiosperms.*—Due to the fact that vessels or tracheae in the Angiosperms developed from a series of subsequent tracheides, a considerable number of tracheides lost their original functions and changed into anatomic elements performing other functions, especially mechanic ones. In the course of the development of different angiospermous groups the organization of vessels, too, has been improved in most various ways. These problems have been dealt with in detail in a great many books and papers (see, e. g., bibliography in K. Esau 1950 and A. L. Tachtajyan [Tachtadžjan] 1948). It has been made clear that the improvement of certain elements, e. g. vessels need not be accompanied to the same extent by the improvement of other building elements in the xylem part, or vice-versa. This is the reason why, the more archaic character is retained by a certain plant, the more such primitive elements are contained in its wood. So far as the vessels are concerned, this applies to the orientation and mode of perforations in their cross walls as well as to the diameter and length of their members. Other important circumstances of this kind can be deciphered from the presence and character of libriform fibres, xylem parenchyma and medullary rays, distribution of vessels in the wood and their relation to the groups of the xylem parenchyma. In studying all these details we often come to see that many of these phenomena were greatly accelerated by the adaptation to outside conditions (see, e. g., the comparatively perfect character of vessels in many amentiferous types contrasting with an imperfect development of libriform fibres (e. g. the *Betulaceae*). This may be in connection with secondary centres of distribution (so characteristic just of the amentiferous plants). Although the xylem part of the bundles presents so many combinations that a correct evaluation as to the archaity of different plant types is sometimes very difficult, taxonomers pay much attention to the structure of wood.

In estimating the archaity of different plant types, the phloem part is given far less care than should be done. It is not until in the Angiosperms that the building elements, present in the phloem part of vascular bundles, marked a more intensified evolution and improvement. Main building elements of the phloem, the sieve-tubes, were not yet appropriately developed, e. g., in the representatives of the Devonian group *Psilophytineae* or in the tree-like Permo-Carboniferous representatives of

group *Lycopodineae*, whereas their tracheides had long before borne various kinds of sculpturings. Nor do the very much advanced gymnosperm types, the tracheides of which reached the most progressive stages in evolution (bordered pits enclosing the tori) show any signs of forming typical sieve-tubes. As a matter of fact, it is therefore in the Gymnosperms that the entire process of gradual development of the phloem building units can clearly be perceived. This problem has been studied so much (see K. Esau or L. L. Tachtajyan [Tachtadžjan] l. s.), that the voluminous literature affords rather a clear picture of the taxonomic value both of the xylem and the phloem. It is evident that the phloem sieve-tubes developed quite separately from, and, to a great extent, independently on, the development of the xylem, especially that of its vessels (notice, e. g., the very primitive sieve-tubes, as compared with the extremely advanced vessels in the amentiferous plants). Moreover, if we follow this process in different plant types, we are more or less inclined to think that the evolution of the phloem depended far less on the outside influences than did the development of xylem vessels and that it corresponds far better to the actual degree of progressivity in the general evolution. It clearly reveals that herbaceous elements, when compared with their woody relatives, are of a derived character as the sieve-tubes in herbs are, to some extent, mostly more advanced. However, it is also of interest to note that Monocotyledons, too, embrace types provided with very archaic sieve-tubes (e. g. the Palms), which indicates that they split from their dicotyledonous ancestors at a time when their development was very little advanced. For these reasons the organization of sieve-tubes should be considered as an anatomic feature of the utmost importance for the solving of taxonomic problems. In setting up angiospermous evolutionary lines this problem has been given much more attention in this paper than has usually been done.

7. *Problem of reproductive organs (pollen-grains, ovules and embryo sac).*—Pollen-sacs, producing pollen-grains, were, as a rule, very rectilinearly compared with sporangia (or microsporangia) of the series *Filices-Pteridospermae-Cycadales*. Some detailed researches, however, clearly revealed that this relation is probably too remote (E. C. Jeffrey and R. A. Torrey), because in the just-mentioned plant series various dehiscence mechanisms of these organs always arise from surface tissues, whereas those of the angiospermous pollen-sacs have their origin in inner tissues, because they are often directly connected with vascular tissues and only secondarily, due to the reduction of surface tissues, come up almost to the surface. In this respect a certain analogy can be found in different coniferophytes (also in the genus *Ginkgo*). This seems to be another convergent phenomenon occurring with strictly terrestrial types in contradiction to the whole series *Filices-Pteridospermae-Cycadales* which is of a hygrophilous nature and only gradually has assumed a more or less terrestrial habit. At the same time, this confirms the correctness of our supposition that Angiosperms must have split from their ancestral stock in very early times, perhaps already in a psilophytoido-filicinean stage.

Angiospermous pollen-grains attained an unprecedented variety in forms. In types which preserved a considerably archaic character they

are rather similar in form to those of some ancient (even Palaeozoic) Pteridosperms. This, too, supports the above-mentioned theory. Besides, a great number of pollen-grains showing angiospermous character and dating from the older Mesozoic (the Jurassic in Scotland, in Scania [southern Sweden], in Caucasus, in Fergana [Central Asia]) and even records of grains, provided with several apertures, from the Lower carboniferous (Naumová's records from the Moscow coal district) clearly point to the fact that the ancestors of today's Angiosperms had existed long before this group fully appeared in Cretaceous deposits. It was not until recently that the arrangement of the pollen-grain sculpturings as well as the composition of their membranes have attracted due attention on the part of taxonomers, and even today some systematists are rather sceptical about these phenomena. It cannot, however, be denied that pollen-grains clear up many uncertainties in the affinities of different plant types, although we know very well that their development in different evolutionary lines may have taken parallel courses (see R. P. Woodhouse 1935, 1936, G. Erdtmann 1952). The setting up of large taxonomic groups and determining their mutual relations cannot be done without appropriate evaluation of pollen-grains. Then it becomes evident that Monocotyledons generally are far more primitive in the organization of their pollengrains than are the Dicotyledons. This fact is evidently connected both with their relative phylogenetic homogeneity and with a strongly marked specialization for certain rather definite condition of life (geophily, hydrophily, etc.).

Angiospermous ovules no longer betray in any how their various parts came to existence. The function of intercepting pollen-grains, apart from some quite exceptional cases (some representatives of the family *Polygonaceae*, monocotyledonous genus *Butomopsis*) was taken over by covering formations enclosing the ovules, i. e. ovary stigmas. This again points to a strictly terrestrial adaptation. Most frequently the ovules, provided they suffered no reductions of any kind, have two integuments. A number of Angiosperms, however, are known to possess ovules with only one integument. So far, it is not quite certain which of the two cases is more original. Many investigators assume that ovules bearing a single integument underwent reductional changes. Though with many plants especially with many sympetalous ones this seems to be very probable, there is no convincing evidence in support of the view that both the types might not have existed side by side since the very beginning. In any case, apart from some exceptions (e. g. the *Umbelliferae* among choripetalous plants, or again the *Ericaceae* among the sympetalous plants), the presence of one or two integuments suggests the four well known sets of Angiosperms: the set of apetalous, as well as sympetalous, plants on one side, and the rest of Dicotyledons (all choripetalous) together with the Monocotyledons on the other. This grouping, evidently unnatural in many respects, is clearly due to convergences and parallelisms that must have indisputably played great part in development. Minor details in the ovule structure, e. g. the so-called eusporangiaty and tenuinucellaty, the character of the tapetum tissue, etc., have apparently to be interpreted in a similar way. In this respect many cases of reductions and derivations

can be found especially with the sympetalous types. It, however, is necessary to point out that, in contradiction to certain indisputable marks of intensive derivation, they show here strongly archaic features in their external, as well as floral, morphology.

8. *Some important problems as to the morphology of angiosperm flower.*—Innumerable books have been published by morphologists, anatomists, and ontogenists on the nature of angiospermous flowers. Their most contradictory opinions are not to be discussed in this brief summary. According to the present state of knowledge, based especially on anatomic details of the receptacle and various floral organs, nothing at all seems positively to indicate an axile character of any floral organ. All the data so far available point either directly to the leafy nature of these organs or make such an explanation acceptable even in considerably disputable cases. Different kinds of reductions and arrangement of reduced florets into various dense inflorescences may, of course, have given rise to formations resembling simple flowers. In this case separate florets may be represented by only one stamen or one ovary which assume the position of axillary shoots (*Cercidiphyllum*, *Salix*). There is not, and cannot, be any doubt that angiospermous flowers represent simple shortened shoots provided with adequately arranged perianth leaves and sporophylls of a leafy nature. Yet there are so many varieties in the behaviour of these organs that recently there arose a theory about a double nature of angiospermous flowers (Lam, Emburger, Kuzněcov, etc.). Some palaeobotanists distinguish two different types of Angiosperms, one arising from coniferoid ancestors and one, from some cycadoid stock; others introduce here the notion of stachyosporry and phyllosporry. Greguss assumes three such basic types at all. This would, of course, mean that Angiosperms have at least a double origin. If we consider them to be a specifically macrophyllous plant group, as stated above, such considerations admitting a double basically different nature of their flowers are becoming quite absurd. All the phenomena which may make such interpretations acceptable (e. g. different behaviour of stamens or carpels in ontogeny, their position and their mutual relations in their maturity, different nature of petals, branched stamens, etc.) must be studied without any prejudice, i. e. from the same points of view as we have done when considering the origin and modification of assimilating leaves. It should be realized here, too, that sterile assimilating leaves as well as fertile leaves or sporophylls necessarily had to undergo similar changes when the whole plant was becoming adapted to strictly terrestrial conditions, i. e. here, too, the development became arrested on a neotenic stage to allow, later, the appearance of forms of growth quite different from those present in their relatives which persisted to live in decidedly moist conditions. And it certainly depended very much on the extent of phylloidization to which their general character and organization, no doubt originally strongly telomoid, had been subjected, before they passed to conditions strictly terrestrial. Besides, the organization of many primitive Ferns from the transition periods of the Devonian to Lower Carboniferous shows that, after the differentiation of macrophyllous fronds into sterile leaves taking over exclusively assimilating function and into leaves bearing

henceforward reproductive organs, the sterile assimilating leaves and the fertile sporophylls (both of macrophyllous character) very probably began to develop quite independently in their own way. In spite of their originally common basis (the great telom system with a lateral orientation and a tendency towards a limited growth), angiospermous assimilating leaves and sporophylls cannot, therefore, be of the same morphological value. In view of the fact that some fertile floral organs may secondarily lose their fertility and change into sterile parts (e. g. stamens into staminoida or perianth leaves), the assumption that many floral parts, particularly some perianth leaves may be a reductional product of sterile assimilating leaves as well as of sterilized sporophylls, is certainly fully justified (in many cases also proved by experience). And, in fact, the sepals in plants with two perianth whorls point, by quite a number of features (venation, anatomy of leaf-traces, mode of phyllotaxy), almost indisputably to their originating from assimilating leaves. The origin of perianth leaves or petals, however, is quite a different matter. They very often rather distinctly show (Water-lily, Rose, etc.) that they arose from sterilized stamens. For that reason they share with them analogue leaf-trace anatomy, their venation for the most part differs from that of sterile leaves and is rather dichotomously branched; also in other respects their anatomic structure is far more primitive. It seems, however, that such an explanation of the origin of perianth leaves or petals cannot be applied to all cases; this has been specially pointed out by A. J. Lam who based his theory of a double character of the Angiosperms on very such features (as well as, of course, on other phenomena). There are apparently also very many plant types where perianth leaves or petals were brought into existence directly by reduction and adequate arrangement of assimilating leaves which were originally sterile. And it is known that sporophylls in most different ancient plants were often concentrated on certain branches of limited growth with no sterile leaves, whereas in others, although closely related, the same shortened axes displayed both sterile leaves and sporophylls, often alternating (e. g. in the group of the Palaeozoic *Equisetales* the strobili of the order *Equisetites* had only fertile sporangiophores, whereas those of the genus *Calamites* bore alternating whorls of both sterile leaves and sporangiophores). Even here, in the angiospermous prototypes, both possibilities are to be assumed: on the one hand axes shortening into flowers provided exclusively with sporophylls some of which changed later into sterile covering leaf-like formations, and on the other hand axes shortening into flowers which bore a great number of sporophylls as well as, on their lower portions, numerous sterile leaflets which soon began to take over the function of perianth leaves so that it was not necessary for the sporophylls to change into perianth leaves by sterilization. In the latter case it is then quite evident that as long as the whole nature of such an arising floral formation was still of a strongly telomoid and relatively plastical character, also the adaptation to terrestrial conditions may have, to some extent, contributed to the descent of sporophylls to positions sufficiently covered by sterile leaves, just as is seen, e. g., in the strobili of the Palaeozoic *Calamites*, i. e. in extreme cases it may have been the cause of an obdiplostemonous or an epipetalous arrange-

ment of the sporophylls. And, in fact, in many angiospermous plants where the supporters of the so-called stachyosporous assumed that perianth leaves were of another origin than the stamens, obdiplostemony or epipetalous position of stamens can be found. L a m and other supporters of the new morphology interpret these phenomena as being due to an axile origin of the stamens, which are therefore situated at the axil of the perianth leaves. In accordance with the result of various anatomical research work, it is, however, more correct to assume that sporophylls and sterile leaflets in question descended as early as the flowers were being formed (there was no shifting of rings of the floral organs in the fully established flowers, as was explained by the classical morphology) to adequate covering positions analogous to those seen in so many cases of Palaeozoic equisetalean strobili. It is, of course, obvious that such position of sporophylls in respect to perianth leaves may be attained secondarily in other ways as well, e. g. probably in the families *Saxifragaceae*, *Primulaceae*, and in some genera of the family *Rosaceae* (just as on the other hand, flowers bearing stamens normally alternating with perianth leaves [e. g. genus *Linum* in the order *Geraniales* or in the families *Nyctaginaceae* and *Batidaceae*, belonging to the centrospermous series] may, by the reduction of a stamen ring, develop from flowers originally obdiplostemonous).

According to the origin of the perianth leaflets or petals two types of angiospermous flowers may be distinguished, even if both these floral types have the same, i. e. euanthium, basis: 1. h o m o g e n o u s f l o w e r s where the shortening fertile shoots originally bore only sporophylls and where perianth leaves or petals developed secondarily by sterilization and re-phylloidization of the lowest sporophylls (i. e. marginal stamens) and 2. h e t e r o g e n o u s f l o w e r s where the shortening shoots bore besides the sporophylls also sterile leaves, in which case the sporophylls did not lose their fertility, nor did they get modified into perianth leaves, because the sterile leaves afforded the necessary protection since the very beginning. To distinguish which of the two flower types really occurs in today's plants is not at all an easy and simple task. A whole series of comparative researches have to be made in the wide affinity spheres, and even the true nature of the flower may not be appropriately determined owing to the fact that the origin of the flowers is of such an ancient geologic past that it is beyond our imagination to conceive how much of their original character was wiped off in the course of their development and by adaptations to strictly terrestrial conditions to attain such features which offer no possibility whatever of recognizing the original state. The above-mentioned reasons lead to the conclusion that many features and characters considered by L a m and other supporters of the "new morphology" to be characteristic of their stachyosporous types are, in fact, characteristic of our types with heterogenous flowers and, vice-versa, properties and phenomena, regarded by the supporters of the "new morphology" as distinctive of their phyllosporous types, are distinctive of our plants with homogenous flowers. From all this, however, it follows that with the Angiosperms the stachyosporous may be considered as an illusory phenomenon. All angiospermous flowers are of phyllosporous and

euanthious character; differences may be assumed only in the nature of the perianth leaves (resp. petals).

Like all originally abundantly divided parts of plantbodies, various floral organs and even entire angiospermous flowers are, during their development, subjected to different reductions and pitiless condensation law formulated by P. B e r t r a n d. This law manifests itself to a specially great extent where the original flowers were most probably of very small dimensions. In this case the number of floral members constantly decreases and the flowers themselves get massed into various inflorescences in which sterile leaves are reduced. This process may go so far that finally only one stamen or one small ovary is all that is left. Then the florets, thus to various degrees strongly simplified and densely grouped on axes of higher orders, finally give rise to formation which are to a great extent and in many respects similar to simple flowers: they have relatively slender stalks, fall off from the main axes as a whole, their bracts may display bright colours. Many of them recall flowers of some archaic plant species provided with relatively elongated receptacles (catkins of some amentiferous plants remind of simple flowers of the ranunculaceous genus *Myosurus*, euphorbiaceous cyathia have the appearance of almost normal simple florets with a small number of floral members and usually low receptacles, many heads or capitula of the *Compositae* or the family *Proteaceae* as well as araceous floral spadices provided with bright spathe often remind of some large flowers with numerous floral organs. In such cases the individual flowers are often unisexual, one of the two sexes being often suppressed as a result of reductional changes. It is not surprising that some botanists, taking for granted that large bisexual flowers developed by reduction from large inflorescences originally, comprising simple florets of one isolated sex, should have explained such processes quite inversely (theory of flowers of pseudanthium character). If, however, all such cases are studied without any prejudice, we finally always come to the conclusion that the original nature of the simple flowers seems to have been bisexual in all cases (frequent remains of reduced organs of the other sex). Many inflorescences already affected by such strong reductions (see, e. g. catkins of some representatives of the family *Juglandaceae* or *Betulaceae*) were again exposed to new reductions, coalescences and plagiotropic arrangement of flowers or of entire miniature axillary inflorescences. These changes resemble very closely the reductions and plagiotropic arrangement of axillary fertile strobili in the female coniferous cones. And this phenomenon greatly contributed to considerations about the relations of some angiospermous plant groups to the coniferous type. It is, however, to be regarded as a mere convergence occurring with angiosperms only in a small number of cases (practically only in some amentiferous types), whereas it became the rule with the *Coniferae*. One of the most extreme cases of such floral reductions which lead to inflorescences similar to mere simple flowers is, apart from the euphorbiaceous cyathia, also the "flower" of the genus *Cercidiphyllum*. Here, on a shortened axis, at the axil of each of more or less opposite bracts looking like greenish dry-membraneous perianth leaves, there is one ovary or one little group of stamens. Everything is so condensed here that even

the shortened portion of the axis bearing these organs makes the impression of being only a slightly elongated receptacle (see also B. G. L. Swamy—J. W. Bailey 1949). It is not surprising that this inconspicuous and tiny type of inflorescence should have been interpreted in different ways; some considered it to be a type of such flowers as are found in the group *Polycarpiceae*, others regarded it as a typical case of the origin of a stachyosporous flower where stamens and ovaries, as axile organs, are still to be found in the axil of bracts. In reality we have to do here only with a very much reduced catkin inflorescence with flowers reduced to only one small ovary or one small group of stamens; these "flowers" cannot be compared with those of the genus *Trochodendron* or with any other type of flowers found in the archaic orders *Magnoliales* or *Ranunculales*.

V. General Process in the Development of the Angiosperms and Their System in the Light of Considerations Discussed in Sections II and IV.

From considerations stated in section II it follows that Angiosperms arose from some ancestors standing somewhere on the boundary of *Profilicineae* (e. g. *Coenopterideae*) and *Pteridospermae*, as some strictly terrestrial evolutionary branch, parallel with the more hygrophilous evolutionary series *Pteridospermae-Cycadeae-Gnetineae* (see Fig. 1). They passed over to angiospermy at about the close of the late Palaeozoic or at the beginning of the early Mesozoic at a time when different groups reveal a general tendency towards concealing ovules into closed receptacles. It is the late Triassic and Jurassic that are to be considered as the period when the splitting of this plant element into a whole series of independent groups (orders, families) took place, because in a more advanced phase of the Lower Cretaceous many of these begin to appear in such a form which differs in nothing essential from the types of today. This short period excludes any possibility of setting up a long and complicated pedigree, as is so often assumed in illustrating their phylogeny or their mutual relationships. The entire splitting of the ancestors of the present-day angiosperms could not have happened in the form of a gradual and slow separation of more and more advanced forms, as can be traced in the development of the Ferns where the process of separating was going on successively from the Devonian till the Cretaceous, but it must have occurred very quickly, as if on a sudden, probably at the time when the angiospermous ancestors were penetrating into strictly terrestrial areas, which were the result of the Hercynian mountain-forming processes of the lower and the middle phase of the Carboniferous. The Angiosperms most probably represent as integral and suddenly segregated an evolutionary branch as are, e. g., the *Bennettitales* in the Mesozoic. The *Bennettitales* reached the zenith of their luxuriance earlier, i. e., as early as the Triassic, Jurassic and Lower Cretaceous, because they came to existence most probably nearer, or even directly in, low-land or moist basin areas. The Angiosperms on the other hand, as an element originating in strictly terrestrial areas, descend to sedimentary areas comparatively late to attain

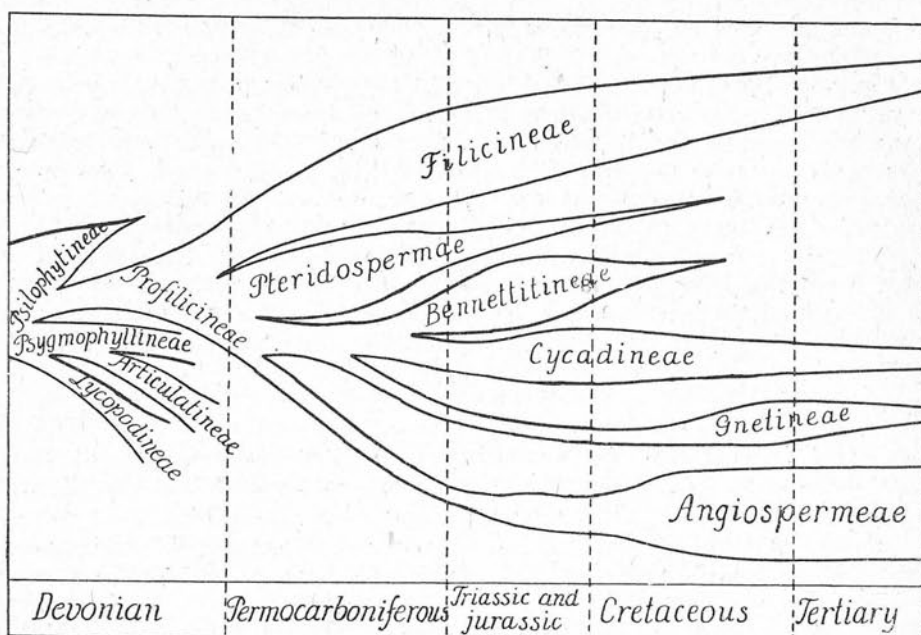


Fig. 1.

Schema vývoje vyšších rostlin (Telomophyta) ukazující vztahy angiospermů k makrofilní vývojové větvi.

Scheme of the evolution of the higher plants (Telomophyta) showing the relations of the Angiosperms to other macrophyllous evolutionary lines.

here their maximal distribution with great delay, only after the extinction of the bennettitalean element; their descent to the sedimentary basins depended to a great extent on the denudation of hilly and mountainous areas. In its final phase this whole process may have been accelerated by the beginning fluctuation in climatic conditions brought about by the initial stage of the Alpine folding, which, of course, did not reach its maximum until the Tertiary.

The above-mentioned reasons make us assume that the prototype of the Angiosperms very early and within a comparatively short period split into a greater number of evolutionary trends forming simultaneously types with homogenous flowers and types with heterogenous flowers. The more did the cladodification (foliarization) of their telomoid organs develop, the greater progress was certainly achieved by the types bearing homogenous flowers. During the older phase of the Mesozoic the trends which thus came into existence seem to have gradually and in some genealogic sequence given rise to a number of evolutionary branches which we consider as definite orders and families. This process must have come to an end in the older phase of the Lower Cretaceous (by about the period of the Cenomanian stage). Accordingly, the following three evolutionary periods are to be assumed for the origin and development of the angiosperm

element: 1) some rather preparatory period during which their common prototype passed over to strictly terrestrial areas, adapted itself to the new conditions and perhaps simultaneously formed primitive closed little ovaries from entire carpels, affected by a considerable reduction, 2) aggregation of reduced sporophylls to primitive flowers of apocarpoid character and apparently simultaneous definitive formation of some fundamental plant types which became the basis of the fundamental evolutionary trends, 3) during the older Mesozoic (the Triassic, the older phase of the Jurassic) if not before, there must have taken place the gradual development as well as splitting of the fundamental trends and the branching-off of different specially adapted types (e. g. types adapted for colder climatic conditions, for moist conditions or for directly aquatic environment, various xeromorphoses and saprophytic, parasitic as well as insectivorous types) and of most sympetalous types. Among the separate fundamental trends, the sympetalous types, after all, represent only a further stage of development in which the young reproductive organs become enclosed as best as possible to be protected against the dry conditions of strictly terrestrial environment.

In the last of the three periods also a gradual progress in the arrangement of the flowers must certainly have taken place. The flowers so markedly characterize the different angiospermous plant types that they belong to the most important phenomena on which the taxonomy of Angiosperms has always been based upon. Here, too, as shown by the floral morphology, three main phases are to be assumed: 1. condensation of floral organs in an indefinite number and their spiral distribution on the shortening receptacle; 2. reduction in the number of floral organs with a tendency towards their descent in a whorl-like manner and a mutual coalescence of small ovaries; 3. transition from an indefinite number of floral members to a strongly reduced and often quite definite number of members descending into conspicuous rings; this process is mostly accompanied by the hollowing-out of the receptacle and a gradual submersion of fertile members (inferior ovaries).

This whole complex course of evolution affecting the arrangement of the flowers was simultaneously, yet not quite to the same extent accompanied by a successive disappearance (due to reduction) of the seed endosperm, a gradual complication of pollen-grain sculpturings and an improvement of anatomic features of the vascular bundles.

All the separate evolutionary trends and their lateral lines did not, of course, pass through all the three above-mentioned phases. Sooner or later, some of them became arrested on the very first or the second stage without reaching more advanced stages. It may have been of consequence whether they had other chances of adapting themselves to the changing life conditions. And so far as the plant types had no longer the necessary plasticity in either respect, they were even becoming extinct. This is confirmed by palaeontological evidence, e. g., when the flora of the middle phases of the Cretaceous is compared with the floras of the older Tertiary. At the same time also types adapted to quite special life conditions were coming sporadically into existence; we can consider them as a series of lateral derivatives, which, however, due to their one-sided evolution and

too one-sided adaptation to certain special conditions, lost the power of undergoing further development.

As the development and improvement of different qualities and characteristics are not fully parallel phenomena, it is evident that the representatives of the three mentioned evolutionary stages cannot be defined precisely. The types that became arrested on the first evolutionary stage may, in some of their features, approach the character of the types fully reaching the second or even (in some cases) the third stage, and, viceversa, the types that in many essential characteristics attained a more advanced stage (the second or the third) may retain certain features characteristic of the most primitive, first stage (e. g. the little advanced types of the order *Rosales*, most representatives of which reached the third evolutionary stage; resemble in many respects very progressive representatives of the order *Ranunculales*).

Since the beginning of the late phase of the Lower Cretaceous (when Angiosperms really appear in larger numbers) we cannot speak about any further formation of substantially new types. Various plant remains from the Tertiary and the late phase of the Cretaceous show that in this period there was a general tendency towards the distribution of certain more or less already fixed plant types in accordance with the gradually changing climatic conditions as they were brought about by the gradual cooling down of the earth from the poles towards the equator and in accordance with the formation of definite climatic zones. It was more or less the formation of secondary centres of distribution of different derived woody plants, adapted to colder or altogether less favourable life conditions and chiefly a continually increasing development of herbaceous derivatives which took place in this period. Nevertheless, we may place the origin and development of one new type, although not quite new from morphological and taxonomical point of views, namely the formation of arctic and high-mountainous derivatives, i. e. angiospermous herbaceous elements adapted to very long winters and considerable transitory sheets of snow. Without dispute the origin of these plants was due to the formation of extremely cold arctic areas and to the Alpine earth movements by which the earth's crust was uplifted into high mountain ranges. As both these phenomena did not exist at the beginning of the Cretaceous, we might perhaps assume a fourth fundamental stage in the development of the Angiosperms. This new derived element of course, appears in this stage after having been split into all the known main taxonomic groups. Apparently only a number of new species, or, at the utmost, genera, came into being, but hardly any higher unit.

In the light of these considerations the problem as to what extent the reconstruction of the prototype of the present-day Angiosperms is possible becomes very burning. As a rule, reference is made to the line of polycarpous types classified so far by the majority of systematists as the orders *Magnoliales* and *Ranunculales*, or simply *Ranales*. As they have a great number of archaic characteristics, they are considered to be the most primitive Angiosperms, and it is therefore in them or in their neighbourhood where the source of development of all the other more progressive Angiosperms is looked for. Most suggestive of this idea have recently

been some plants of considerably relict nature, displaying an extremely primitive character in their stamens or ovaries, and sometimes also homoxylous wood. According to the above considerations, especially considerations concerning the nature of the angiospermous leaf, and, to some extent, also the history of this whole most progressive group, as can be reconstructed on the basis of well established palaeontological data, the present-day state of this group can in no way give us any idea of such a prototype. Only to some extent does this group afford a very indistinct picture of what the representatives of various fundamental evolutionary trends, which segregated from the common prototype and did not develop beyond the first evolutionary stage, may have looked like. This picture is also rather hazy, because the group *Ranales* (in the broadest sense) is a trend which became arrested on the very stage of development where, due to necessary adaptations to successive changes occurring in its environment, it must have undergone considerable alterations. Only the complex of certain basic characteristics indicates to a certain degree what fundamental features it may have had in common with the members of other evolutionary trends, reaching, later on, higher stages of development, when these were passing through the first evolutionary stage (apocarpous floral nature, ovaries bearing large apertures, but no styles, stamens with three leaf-traces and considerable tendency towards cladodification, wood occasionally homoxylous). In other respects, however, the individual trends, when passing over to strictly terrestrial life conditions, must have shown specific peculiarities of their own: it cannot be imagined that the common prototype itself, as some more commonly distributed plant element, should not have been split into certain lower taxonomic units exhibiting their own specific peculiarities, even if, on the other hand, some other reasons (different fundamental features common to all angiosperms, as stated above) lead us to the assumption that the trend represented by the prototype was a very narrow one. All this means that magnolio-ranunculoid type cannot be considered as an actual evolutionary source of the other more progressive angiospermous evolutionary trends. From the whole series of parallel fundamental evolutionary branches it is to be regarded as the one which, of all others, may have lagged behind in evolution. Also acceptable would be the opinion that it represents a type which attained angiospermy relatively late and was for that reason no longer able to reach more progressive evolutionary stages. A relatively strong cladodification of the sporophylls (stamens!) in many types may even be in support of this view (i. e. the descent of such plant types from ancestors where both sporophylls and assimilating leaves were considerably losing their telomoid character and formed to a great extent the leaf lamina itself). The trends which by the close of the Lower Cretaceous reached higher developmental (more progressive) stages (i. e. the second or even the third) are to be considered as being disproportionately more ancient in origin than is the magnolio-ranunculoid type which has so far been regarded as the oldest one. Their past, therefore is literally lost in the unknown. The whole problem of the splitting of the separate evolutionary groups from a common prototype should be conceived quite inversely to what has been indicated by the current genealogic assumptions accord-

ing to which the magnolioranunculoid line is the source of the whole angiospermous group. The assumption suggested in this paper may probably be best illustrated by the synopsis diagram (Fig. 2).

If we accept the above views as to the origin and later development of the angiospermous plant element and take into consideration its various morphological and anatomical peculiarities, as discussed in section IV we get rather a different picture of the fundamental systematic classification and taxonomy of the Angiosperms. First of all, no uniform genealogic survey with the magnolio-ranunculoid group as a starting point can be thought of. It is necessary to set up a greater number of developmental trends showing independent and relatively short pedigrees, trends, many of which split at the very beginning into parallel branches either with homogenous or heterogenous flowers. And then various groups appearing in almost all present systems as groups which could be placed into any single global and rather complicated pedigree only with a good deal of imagination (e. g. amentiferous types, urticaceous plants, centrospermous plants) reappear in this light more clearly as some of those fundamental evolutionary branches which segregated in the far past from the common still hygrophilous prototype and reached, in the course of the older Mesozoic, different stages of progressivity in their development, quite parallelly with the backward and lagging behind magnolio-ranunculoid evolutionary branch. Neither can from this point of view, the set of plants which the modern supporters of the new morphology classify as phylloporous evolutionary branch, be considered as satisfactorily uniform, because its separate lines necessarily lose the connecting link assumed to be found in the magnolio-ranunculoid line. As a matter of fact, this set, too, falls into a series of different evolutionary trends from among which just the magnolio-ranunculoid line represents among the whole series of such parallel lines, the one which reached only the first stage of evolution. The representatives of other parallel evolutionary trends are e. g. *Rhoeadales*, *Canellales*, or *Dilleniales* which reached approximatively the second stage, or cruciferous, roseate, columniferous, guttiferoid, myrtoid plants as well as celastroid, sapindoid and umbelliferous plant groups, which all attained the third stage of evolution. All this necessarily results from the above-stated assumptions concerning the development of the whole angiosperm group, assumptions which we must arrive at, if we consider not only the actual possibilities of the plant development, as can be gathered from the known palaeontologic data, but also the extremely short geologic period which, in the whole history of the evolution of organisms, was allotted to the origin and rise of Angiosperms. Nearest to this conception may perhaps be the opinion expressed by the French botanist Emberger (1944), who, too, suggested a system of a number of parallel partial pedigrees without considering any group as a common ancestral prototype. The outlines of his system, however, are based on absolutely different morphological assumptions which cannot be approved of and which would lead to the assumption of a pronounced and absolutely improbable polyphyletic character of the Angiosperms. Emberger accepts, e. g., the possibility of two absolutely different floral types (stachyosporous and phylloporous), the possibility of axile nature of the stamens or ovary placenta, the

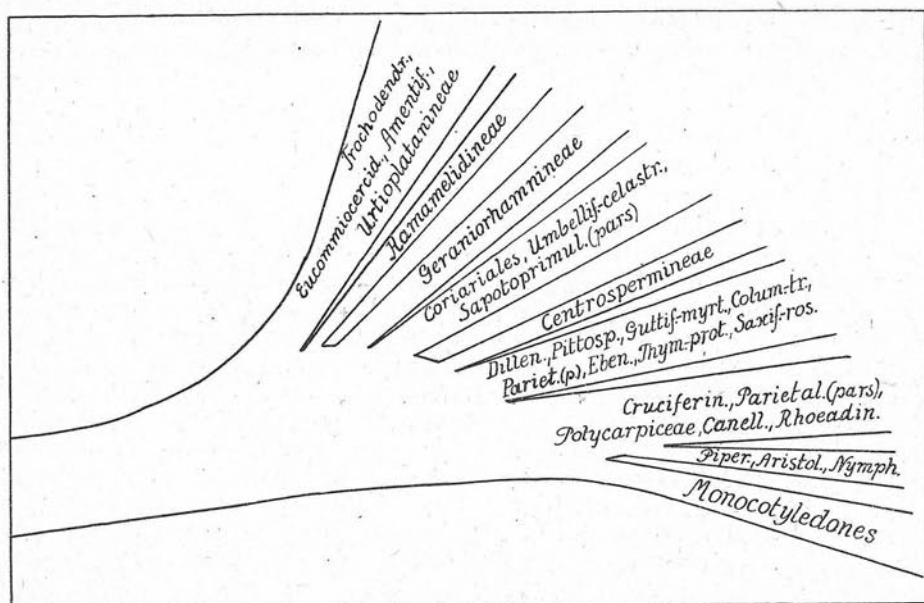


Fig. 2.

Obecné schema naznačující v nejhrubších rysech poměrně náhlý rozpad angiospermické vývojové větve.

General scheme illustrating in the most rough lines the rather sudden disintegration of the angiospermous evolutionary branch.

existence of sterile bracts in the ovary structure of some plants (e. g. centrospermous), and the analogy of some flowers with compound coniferous cones—all these being the phenomena which are in contradiction already with their macrophyllous character itself.

According to a detailed evaluation of the different so far known morphologic, anatomic, and palynologic data the whole angiospermous group can be divided into about six fundamental evolutionary trends (some fundamental evolutionary stocks) with heterogenous flowers (including several relatively rare sympetalous types), about eleven trends with homogenous flowers (together with a series of sympetalous derivatives), two groups of ancient sympetalous plants whose relations to some of these eleven trends with homogenous flowers can be traced today only with greatest difficulty, and a group of Monocotyledons, very clearly linked with a relatively archaic fundamental magnolio-ranunculoid line with homogenous flowers (classified in this paper as the trend Polycarpiceae). The monocotyledonous group itself comprises six rather independent parallel evolutionary trends. Reasons for establishing such a system are briefly given in the following section dealing with various remarks on the separate orders or families, their taxonomic classification, as well as their probable phylogenetic relations.

VI. Remarks on Evaluation of Affinities among the Most Important Angiospermous Orders and Families.

A. Affinities of several dicotyledonous orders or families with very reduced flowers.

1. Amentiferous types.

The following orders and families are to be taken into consideration here: *Juglandales*, *Julianales*, *Garryales*, *Batidales*, *Piperale*s, *Hydrostachyales*, *Fagales*, *Balanopsidales*, *Myricales*, *Salicales*, *Leitneriales*, *Casuarinales*, *Stachyuraceae*, and *Myrothamnaceae*. Their fructification formations, catkins, or various tiny little capitula comprising only small grouplets of stamens or ovaries, arranged in a certain order and provided with protective bracts, have, by different botanists, been interpreted as either inflorescences consisting of more or less reduced florets (according to the classical morphology) or as cases of an initial stage of development of bisexual flowers which come to existence as a result of aggregation of tiny, strongly reduced monosexual flowers (the basis of pseudanthium theory), or, finally, as cases of still imperfect primitive flowers with elongated receptacles. Apart from other phenomena, the last opinion is suggested also by the fact that the flowers very often fall off as a whole, because their receptacle, when compared with the other axes and branches are strikingly slender and of a different nature. It is in the genus *Salix* or *Casuarina* that this phenomenon is perhaps most striking. In other respects, however, the floral nature of the separate elements constituting the catkins is, as a rule, rather well visible, and, moreover, the presence of the rudiments of the other sex clearly proves that sets of strongly reduced, for the most part originally bisexual florets are concerned here. The classical conception of inflorescences of strongly reduced flowers cannot be easily denied. Many cases show even a plagiotropic arrangement of the separate members (florets or even whole shortened axillary inflorescences) of the catkins (e. g. the *Juglandaceae*, *Betulaceae*), which strongly reminds of the reductional conditions found in the female coniferous strobili. This phenomenon seems to have largely contributed to the assumption that some Angiosperms are of a stachyosporous nature.

The orders *Juglandales* and *Julianales*, when compared with other amentiferous plants are conspicuous by their imparipinnate leaves. Their tiny flowers are arranged into simple catkins and contain a good deal of resin substances giving off a very pleasant aromatic scent. In the order *Julianales* the floral structure is radial and the stamens regularly alternate with the perianth leaves. The arrangement of floral members in the genus *Juglandales* offers rather an intricate picture, because especially male flowers of different genera show a different degree of coalescence with the supporting bracts and the plagiotropic adaptation; there is nothing at all that would indicate an epipetalous or an obdiplostemonous position of the stamens; in more distinct cases an alternating position can easily be found. Neither of the orders forms any seed endosperm. Apart from some considerably progressive (e. g. many representatives have simple perforations of vessel transverse walls) characters, both the genera disclose

also many rather primitive features (e. g. sieve-tubes of the first Hemenway stage; many representatives have heterogenous medullary rays). Pollen-grains in the order *Julianales* are more primitive (3-5-7-colporate, or 5-8-aperturate) than in the order *Juglandales* (3-7-porate to 6-16-foraminorate to rugorate). According to Erdtmann the *Julianales* show a closer analogy especially to the pollen of the genus *Pistacia* (the family *Anacardiaceae* from the order *Sapindales*), whereas the *Juglandales* due to a strong derivation, exhibit a considerable resemblance to very much advanced pollen-grains of the families *Betulaceae*, *Myricaceae*, or *Casuarinaceae*. Their fossil record is not very old: they may be traced with more certainty to later phases of the Upper Cretaceous. In view of their chemism, arrangement of leaves, probably homogenous floral character and partly with regard to the pollen nature (especially in the order *Julianales*) they are to be considered as ancient amentiferous derivatives of an evolutionary line leading to the origin of the order *Sapindales*.

The order *Garryales* includes the only genus *Garrya* with flowers arranged into compound catkins. Male flowers display stamens alternating with parianth leaves, ovules have only one integument and seeds contain abundant endosperm. According to Erdtmann, the 3-colporate pollen-grains show closer analogies to the pollen not only of some representatives of the family *Araliaceae* (the order *Umbelliferales*), but also of the order *Leitneriales*. The possibility of a relation to the order *Umbelliflorales* has already been pointed out by K. Prantl and F. A. Novák. In view of the arrangement of the ovaries, this relation is most probably very distant (in the order *Umbelliflorales* the ovaries are already inferior). Although no suitable fossil record is so far available, it is most certain that this order must have split at some very early times from the evolutionary line leading from the common celastro-sapindoid stock to the umbelliferous types.

The order *Batidales* (the only species *Batis maritima*) has opposite leaves of a considerably succulent character (halophilous type) and unisexual flowers (male ones with a rudiment of the gynoeceum) arranged in four-rowed spikelets. It is only male flowers that developed sepals and petals, alternating with four stamens. The ovary, originally two-chambered, becomes four-chambered when mature. The 3-4-colporoidate (to rupo-roidate) pollen-grains are, according to Erdtmann, most similar to the pollen of the centrospermous *Gyrostemonaceae*, and partly of the *Polygonaceae*. The determination of the pollen-grain nature has cast light on the so-far mysterious relations of this order and confirmed the assumed relations to centrospermous types (J. Hutchinson, J. Velenovský) rather than the relations to the family *Papaveraceae* (A. A. Grossgejm) or *Salicaceae* (H. Gamson serodiagnostical grounds); of course, an originally obdiplostemonous type and the loss of their exterior stamen ring have to be assumed here, just as this is to be done with many other centrospermous types (e. g. the family *Nictagynaceae*).

The *Piperales* and *Hydrostachyales*.—In the first order are usually placed the families *Piperaceae*, *Peperomiaceae*, *Saururaceae*, and *Chloranthaceae*, although the *Chloranthaceae* are often by some botanists connected with the order *Laurales*. Many investigators include here also the family *Lacistemaceae*. Today, there is no doubt that the first four fam-

ilies are closely related to the order *Magnoliales* in the broadest sense. This opinion is supported by the mostly monosulcate nature of their pollen grains. Also their anatomy has preserved very primitive features: scalariform perforations of the vessel cross walls, lack of libriform fibres (only tracheides), homoxylous wood in the genus *Sarcandra*. The family *Peperomiaceae* even displays a number of characteristics reminding of Monocotyledons (almost ataktostelic vascular bundles; some types, when germinating, form only one cotyledon). Quite different, however are the conditions in the *Lacistemaceae* where, just as in the mentioned families of the order *Piperales* a strong floral reduction (to only one stamen; one-chambered ovary formed by three carpels) took place; the nature of its ovary and, according to Erdtmann, also the shape of its pollen-grains however doubtlessly reveal a relation to parietal types (its pollen is related particularly to that of the family *Flacourtiaceae* of the order *Bixales*). The *Hydrostachyales* (with the only aquatic genus *Hydrostachys*), just like the *Podostemonales* with which, to the opinion of many investigators (Warming, Hutchinson), they are more closely related, are very strongly adapted to aquatic environment. Engler suggested relations to the *Piperales* or *Salicales*, *Grossgejm* to the *Rosales*. Strong reductions, which are due to aquatic environment, makes the problem very difficult, nor do pollen-grains reveal anything of importance (they are very much reduced, nonaperturate and set up in tetrads). In contradiction to the *Hydrostachyaceae*, however, the *Podostemonaceae* have preserved both flowers and pollen of much less reduced nature (recalling rosaceous plants). In view of the kind of reductional tendencies, the *Hydrostachyales* seem to be more probably related to the order *Piperales*.

The orders *Fagales* and *Balanopsidales* are two rather closely related groups, each of which has taken rather an opposite course of development. They gave rise to many types which formed secondary centres of distribution in temperate zones (Arcto-Tertiary types). So far as flowers are more completely preserved, they have markedly epipetalous stamens which, together with other various characteristics, suggest a heterogenous floral nature. In many respects the anatomical structure of their wood is similar to that of the family *Hamamelidaceae*, but, according to Erdtmann, the nature of pollen differs entirely. If the pollen is to be considered as a distinguishing factor, three more closely related lines can be distinguished here: the family *Balanopsidaceae*, the pollen of which is relatively little advanced (with 3-4- and even 5-colpoid apertures) and of a type rather common also among other dicotyledonous groups, and two more specialized lines namely the *Fagaceae* with a more primitive, 3-6- and even 7-aperturate pollen (colpate, colporoidate and even colporate), and a pair of the families *Corylaceae* and *Betulaceae* with a relatively strongly derived pollen provided with 3-7 equatorial poroid apertures. The order *Balanopsidales* (two genera in New Caledonia) has perianthless flowers and still well developed seed endosperm. In the order *Fagales* the perianth is often preserved and the endosperm missing. The radial floral structure has been retained entirely by its family *Fagaceae*, but only partially by its families *Corylaceae* and *Betulaceae* owing to a frequent plagiotropic orientation or even fusion of the flowers with the supporting scales (analogous process is

found in the family *Juglandaceae* or in female coniferous cones). The anatomical structure of these orders reveal some considerably archaic characteristics (very primitive sieve-tubes of the first Hemenway stage, lack of libriform fibres and, in many representatives, very long vessels bearing scalariform perforations besides other relatively progressive ones: many representatives have wide, short-articulated vessels, simple perforations of vessel cross walls). All this suggests that the types concerned are all of a heterogenous character and must have split as amentiferous derivatives at some very ancient time: their more certain fossil record dates from as early a period as the mid-Cretaceous and they fully developed in the later phase of the Cretaceous. They divided into two fundamental branches (the presentday orders) one of which, the *Fagales*, split further into a more archaic series *Fagaceae* and a more progressive pair *Betulaceae-Corylaceae*. From various phenomena (see below: the orders *Trochodendrales* and *Urticales*) we may suppose that they have certain relations not only to some very archaic woody plants, such as the families *Trochodendraceae*, *Cercidiphyllaceae*, and *Eucommiaceae*, but also, perhaps, to more progressive lines *Urticales* and *Platanales*.

The orders Myricales, Salicales and Leitneriales. — Usually, and especially in older taxonomic systems, these orders are considered as being more closely interrelated (see J. V e l e n o v s k ý, etc.) because of various similarities in floral reductions and in the relations of the flowers to the supporting bracts. So far-reaching are these relations that they very often entirely obscure the original state of the flowers. Like the preceding group, all these three orders are often said to be related to the order *Hamamelidales* (J. H u t c h i n s o n ; F. A. N o v á k, who excludes the *Salicales*). Palynological conditions, recently discovered by E r d t m a n n, however, have shown that the relations between these orders (the same applies to the orders *Balanopsidales* and *Fagales*) and the order *Hamamelidales*, if there are any, are extremely remote to enable us to see them today. In the *Myricales* the pollen has been found to be 3-porate, mostly approaching that of the families *Betulaceae*, *Corylaceae* and *Casuarinaceae*, whereas a 3-colporoidate pollen (*Salix*, *Chosenia*) or very much derived, nonaperturate (*Populus*), very close to that of some parietal types (*Flacourtiaceae*, *Tamaricaceae*) was ascertained in the order *Salicales*, and a 3-6-colporate one, similar to that of the representatives of the families *Juglandaceae*, *Garryaceae*, or *Coriariaceae*, in the order *Leitneriales*. This shows that all these three orders arose as amentiferous derivatives from three absolutely different evolutionary trends. It is of interest that such possibilities have already been suggested from purely morphological points of view (H. H a l l i e r, A. L. T a c h t a j j a n [Tachtadžjan]; the arrangement of seeds in the genera *Salix* and *Populus* reminds that found in the order *Tamaricales*, and the wood of the order *Salix* recalls that of the genus *Idesia*). Their splitting must, of course, have taken place at a very remote period. Fossil record of the genera *Myrica*, *Salix*, and *Populus* date from as early times as the middle phases of the Cretaceous. As regards the anatomic structure, they have preserved a number of very archaic characteristics (there are mostly primitive sieve-tubes of the first Hemenway stage; many representatives have terminal parenchyma). Upon the whole, it is clear

today that the order *Myricales* is related to the orders *Balanopsidales* and *Fagales*, the order *Salicales* to the order *Parietales*, and the order *Leitneriales*, to the orders *Celastrales* and *Sapindales*.

The order Casuarinales.—Its present-day distribution shows that it represents a relict of very ancient floras (apparently dating already from the mid-Cretaceous); palaeontology may, however, never be able to confirm this assumption because of the considerably xeromorphous character of this plant type (its remains had no chance of entering into fossiliferous series). Its flowers, strongly reduced (to only one stamen or one ovary) betray nothing about the original floral state. Its considerable progressivity manifests itself also by the loss of the seed endosperm. According to Erdtmann's palynological researches it bears most analogies with the family *Betulaceae*, fewer with the family *Myricaceae*. To a certain degree, its ancient origin is proved by some archaic anatomical characteristics (very primitive sieve-tubes of the first Hemenway stage, lack of libriform fibres, and heterogenous medullary rays). Like the order *Myricales*, also this order seems to be probably linked in some way with the orders *Balanopsidales* and *Fagales* and represents a very highly specialized xeromorphous derivative. In a sense, the same has been suggested by J. Velenovský on purely morphological grounds.

The flowers of the families Myrothamnaceae and Stachyuraceae form upright and dense little racemes or spikelets of catkin appearance. In the family *Myrothamnaceae* the perianth is missing, the flowers are dioecious, leaves stipulate. As to the *Stachyuraceae*, the flowers are bisexual, stamens normally alternate with petals and leaves are exstipulate. In both the families the ovules are placed at the interior angles of the ovaries. The seed endosperm is well developed. According to Erdtmann, the pollen of the family *Myrothamnaceae* has three colpoids and forms tetrads similar to those found in some genera of the family *Monimiaceae* (*Laurales*). In the family *Stachyuraceae* the pollen is free, 3-colporate (to 4-ruporate), recalling in some respects the pollen of the representatives of the family *Flacourtiaceae* (the order *Bixales*; the placentation is, of course different). The general nature of the flowers is most probably homogenous (this is certainly the case in the *Stachyuraceae*). Both the families are most often believed to be related to the order *Hamamelidales* (J. Hutchinson). For some morphological reasons and in accordance with palynological conditions, the family *Stachyuraceae* is recently considered as being related to the order *Bixales* (especially to the family *Flacourtiaceae*). With regard to the family *Myrothamnaceae*, we must not forget that the family *Hamamelidaceae* also discloses some characteristics recalling the family *Monimiaceae* (F. A. Novák). As the same cannot be said with reference to the pollen-grains, the problem of affinity of both these families cannot, for the time being, be solved definitely; it is, however, rather probable that the family *Myrothamnaceae* may distantly be related to the order *Hamamelidales*, and the family *Stachyuraceae*, to the order *Bixales*.

The brief outline of the above-mentioned reasons leads to the conclusion that amentiferous plants do not represent any uniform trend, but a number of more or less convergent and at the same time quite independent

amentiferous derivatives originating from most different angiospermous evolutionary trends or lines:

the order *Salicales*, the families *Lacistemaceae*, and apparently also *Stachyuraceae* are linked up with *parietal evolutionary series*;

the orders *Piperales* and *Hydrostachyales* are related to the evolutionary trend *Polycarpiceae*,

the orders *Jaglandales*, *Julianales*, and *Leitneriales* show relations to celastro-sapindoid evolutionary lines,

the order *Garryales* is connected with the umbelliferous trend,

the family *Myrothamnaceae* may probably be related with the order *Hamamelidales*,

the order *Batidales*, according to all appearances, is most probably allied to centrospermous plants,

the orders *Balanopsidales*, *Fagales*, *Myricales* and *Casuarinales* represent a very individual amentiferous trend (*Amentifereae* in a strict sense) of evidently ancient origin, linking remotely with the relationship of the genera *Trochodendron*, *Cercidiphyllum* and *Eucommia*.

The first five cases may most likely be supposed to produce flowers of a homogenous nature, the last two, flowers of heterogenous character.

2. The family *Cercidiphyllaceae* (Fig. 3 and 4).

This family comprises the only still living genus *Cercidiphyllum* (*C. japonicum*) indigenous to Eastern Asia. It is most frequently considered to be a member of the order *Magnoliales* and related to the family *Trochodendraceae*. Small head-like and long-stalked floral formations are dioecious and made up of dry-membraneous scale leaflets standing before either a greater number of stamens (about 15—20) or several (even more than six) free one-carpel ovaries maturing into more-seeded follicles. Seeds contain abundant endosperm. The anatomical structure of wood is rather archaic: the wood has no libriform fibres, its very long vessels are diffusely scattered, have very oblique cross walls with scalariform perforations; their ends are pointedly protracted and provided with spiral sculpturings. The wood parenchyma is apotracheal, relatively scanty and terminal, the medullary rays heterogenous.

As has recently been pointed out by G. B. L. Swamy and I. W. Bailey, it has long been known that the separate floral members of the small heads are not arranged successively in a normal way, in spirals or rings, but each separate ovary as well as each separate grouplet of stamens is placed in the axil of the separate scales. Floral scales are placed in pairs approximatively opposite one another on an elongated receptacle. If a separate scale is torn out, the respective ovary or grouplet of stamens gets loose. This, of course, signifies that these floral formations cannot be looked upon as normal polycarpous flowers, as is usually done; they have to be considered as very short long-stalked simple catkins with perianthless florets, reduced to a single one-carpel ovary or one small grouplet of stamens. This nature of theirs is clearly visible when they are compared with young axillary sterile shoots (see Fig. 3 and 4). At the base of

both the axillary sterile shoots and floral stalks three massive scales a, b and c are placed. The scales a and b stand opposite each other, whereas opposite the scale c we find a normally developed sterile leaf of the sterile shoot, the stipules of which are not normally developed (long pointed) but intrapetiolarly fused into a dry membranous formation [α], cut in front into irregular narrow and short lobes. Next leaves of the

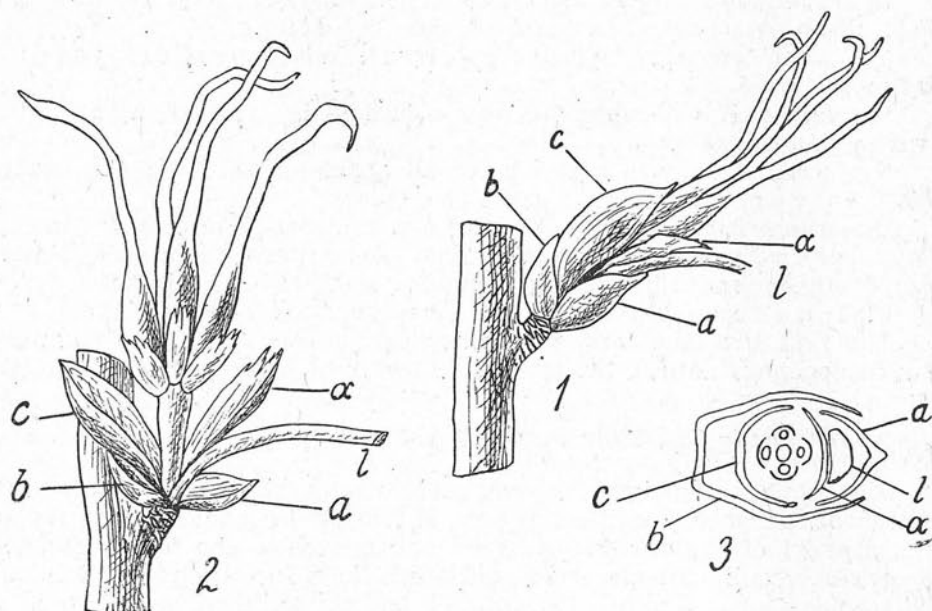


Fig. 3.

Cercidiphyllum japonicum: Samičí „květ“ (1,2) a jeho diagram (3); a, b, c — šupiny obalující „květ“ v pupenu; 1 — řapík řádně vyvinutého listu pod „květem“, α — jeho palisty. — Slabě zvětšeno.

Cercidiphyllum japonicum: Female „flower“ (1, 2) and its diagram (3); a, b, c — scales enclosing the young „flower“ bud; 1 — petiol of the well developed leaf subtending the „flower“, α — its stipule. — Slightly enlarged.

sterile shoots stand in alternate pairs and their stipules are normal. The long floral stalk is, of course, leafless, but the perianth leaves, placed at its extremity in alternate pairs, are quite similar to the mentioned dry-membranous scale (α). They obviously represent supporting leaves reduced to mere fused stipules, at the axil of which are found those extremely reduced florets.

Erdtmann states that the pollen of the genus *Cercidiphyllum* bears no closer resemblances to the pollen of the order *Magnoliales* (in a strict sense) or the order *Hamamelidales* or even any amentiferous families. He found most analogies in the genus *Eucommia* and to some extent, in the genus *Trochodendron*.

Palaeontologically the genus *Cercidiphyllum* is regarded as a very ancient type, known to us already from Cretaceous formations (North Ame-

rica), nor is it impossible that the imprint of the angiospermous leaf recorded by A. C. Seward from the English Jurassic may, in certain respects, be referred to it (rather than to the genus *Populus*, as was Seward's own opinion). The description of fossil fruits of this genus

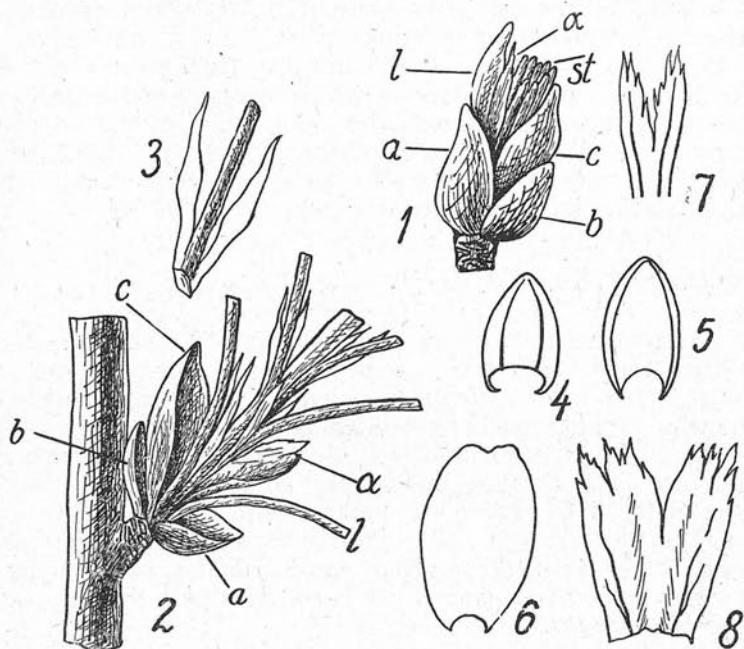


Fig. 4.

Cercidiphyllum japonicum:

Obr. 1. Mladý samčí „květ“: a, b, c — šupiny obalující „květ“ v pupěnu; 1 — část mladého listu nasedajícího pod „květem“, α — jeho palist; st — z pupene vyčnívající skupina tyčinek.

Obr. 2. Basální část mladého sterilního prýtu: a, b, c — šupiny obalující rašící pupen v mládí; 1 — řapík prvního dobře vyvinutého listu s intrapetiolárně srostlými palisty α ; řapíky dalších listů mají palisty normální, nesrostlé.

Obr. 3. Base řapíku listového s normálně vyvinutými palisty.

Obr. 4, 5, 6. Tvar šupin a, b, c obalujících v mládí pupeny „květů“.

Obr. 7. Dvojitý palist listu nasedajícího pod „květem“.

Obr. 8. Tvar nepatrných „okvětních“ lístků v „květech“.

Vše slabě zvětšeno.

Cercidiphyllum japonicum:

Fig. 1. A young male „flower“: a, b, c — the scales enclosing the „flower“ bud during its young state; 1 — part of the developing leaf subtending the „flower“, α — its stipule; st — stamens.

Fig. 2. Basal part of a young leafy shoot: a, b, c — scales enclosing the young shoot in the bud; 1 — petiole of the first leaf with its intrapetiolary connate stipules α ; all other petioles are provided by 2 normal stipules.

Fig. 3. Base of a leaf petiole with both stipules.

Fig. 4, 5 and 6. The shape of the scales enclosing young „flowers“.

Fig. 7. The intrapetiolary connate stipules of the leaf subtending the „flowers“.

Fig. 8. The shape of the very inconspicuous „perianth“ scales of the „flowers“. All fig. slightly enlarged.

revealed that the axes of headlike inflorescences ("floral receptacles") are much longer in many fossile types than they are in the living species, moreover even branched axes are referred in the Upper Cretaceous species *Cercidiphyllum ellipticum* Newb. (R. W. Brown, 1939).

These are the reasons why the genus *Cercidiphyllum* cannot at all be considered as a member of any polycarpous family, but as an entirely individual type, representative of an entirely independent order *Cercidiphyllales* with evolutionary tendencies which strongly converge to amentiferous types. It is somehow related with the families of the *Eucommiaceae* and more remotely also with the family *Trochodendraceae*. It is perhaps in this way that it may have some (of course extremely remote) relations to the group *Amentiferae* in a strict sense.

3. The family *Trochodendraceae*.

Besides the above-mentioned genus *Cercidiphyllum*, also the genera *Trochodendron*, *Tetracentron*, and *Euptelea* are usually included into this family. The first two are markedly homoxylous, the last, normally heteroxylous. The whole family used to be reckoned among the order *Magnoliales*. Recently (also F. A. Novák), however, due to a very different morphological nature of both flowers and vegetative parts, the separate genera are often considered to represent independent relict families (*Trochodendraceae*, *Tetracentraceae* and *Eupteleaceae*). Some botanists also suggest possible relations to the order *Hamamelidales*, because the flowers of at least some of them have very little in common with the representatives of the order *Magnoliales*.

In the flowers of the genus *Tetracentron* the position of the stamens (four in number) is epipetalous and the ovaries, alternating with the stamens, are fused into a primitive syncarpous gynoecium. As to the genera *Trochodendron* and *Euptelea*, perianth leaves are missing and bisexual flowers have a greater number of stamens, their ovaries form a ring in the centre and slightly coalesce laterally in the former genus, whereas they are free and stalked in the latter. According to Erdtmann, the pollen in the genera *Trochodendron* (3-colpate to colpoidate) and *Tetracentron* (3-4-colpoidate) is rather similar and greatly differs from that found in the genus *Euptelea* (of 6-rugate type). The stigmas in the genera *Trochodendron* and *Tetracentron* are well developed, which is not the case of the genus *Euptelea*. From all this it follows that the genus *Euptelea* may hardly have any closer connection with the genera *Trochodendron* and *Tetracentron*. This is also confirmed by a different structure of the axis nodes. The form of the stamens and arrangement of the ovaries in the genus *Euptelea* is, to some extent, reminiscent of the condition in the family *Winteraceae*.

On these various grounds the genera *Trochodendron* and *Tetracentron* are to be considered to represent an entirely independent order *Trochodendrales* which has no closer relations to the order *Magnoliales* and the whole trend *Polycarpiceae*. Its affinities (of course rather remote) are to be looked for among the *Amentiferae* (in a strict sense), the genera *Cerci-*

diphyllum, *Eucommia*, and perhaps the order *Urticales*. On the contrary, again, the genus *Euptelea* shows very clear relations to the group *Polycarpiceae* and also seems to be related to the family *Winteraceae*.

4. The genera *Eucommia* and *Rhoiptelea*.

Today these two genera represent two relict elements, characteristic of the East Asiatic flora. From the palaeogeographic point of view, they belong to the elements of the Arcto-tertiary flora largely distributed (especially *Eucommia*) in the Tertiary temperate zone of the Northern Hemisphere, where, like various amentiferous types, they formed their secondary centres of distribution. The genus *Eucommia* has strongly reduced perianthless flowers of one sex only (a greater number of stamens or one ovary). For this reason it is often connected with the family *Hamamelidaceae* where the tendency to such reductions is rather apparent. According to Erdtmann its 3-colporoidate pollen, even in more delicate sculpturings, reveals far closer analogies to that of the genus *Cercidiphyllum*, and more remote to that of the genus *Trochodendron*. The genus *Rhoiptelea* to some extent reminds of nut-trees; it has similar imparipinnate leaves. The stamens of its florets, however, have an evidently epipetalous position. According to Erdtmann its 3-colporate pollen is most reminiscent of the pollengrains in the family *Betulaceae*, rather less also to the pollen of the family *Ulmaceae*. Both have winged fruits recalling elm achenes. The endosperm is abundant in the genus *Eucommia*, but it is missing in the genus *Rhoiptelea*.

All this signifies that the genus *Eucommia* represents an entirely independent relict type (classified in this paper as the order *Eucommiales*), close to the order *Cercidiphyllales* and thus also *Trochodendrales*. The genus *Rhoiptelea*, too, has to be regarded as an independent relict (the order *Rhoipteleales*), rather more closely related to the more advanced types, such as *Amentifereae* (in a strict sense) or even to a still more advanced evolutionary line, the order *Urticales*.

B. Remarks on the Six Fundamental Evolutionary Dicotyledonous Trends, with Flowers Assumed to Be of a Heterogenous Character (Fig. 5—6).

According to the state of progressivity in the floral structure and anatomic character of vascular tissues (particularly according to the relative progressivity of sieve-tubes), the six evolutionary trends, assumed to have flowers of a heterogenous character, may be divided into three groups representing the evolutionary stages they have attained until now (as a matter of fact, already by the close of the Mesozoic).

1. Evolutionary trends arrested on the first stage: *Trochodendrineae* (Fig. 5).

For reasons stated in the preceding section the first group, whose plant types reached, and became arrested on, the first, most archaic stage, embraces the only order *Trochodendrales*

(i. e. the genera *Trochodendron* and *Tetracentron*) as the evolutionary trend *Trochodendrineae*. With great many features, the whole trend (or its present-day relicts) converges to the trend *Polycarpiceae* where its flowers are supposed to be of a homogenous nature. This has certainly been the reason for assigning its representatives directly to the order *Magnoliales*.

2. Evolutionary trends arrested on the second stage.

The second group, i. e., types which became arrested on the second evolutionary stage, includes three evolutionary trends: the *Eucommio-cercidiphyllineae* (with the orders *Eucommiales* and *Cercidiphyllales*), *Amentiferineae* (with the orders *Balanopsidales*, *Fagales*, *Myricales*, and *Casuarinales*), and *Urtico-platanineae* (with the orders *Rhoipteleales*, *Platanales* and *Urticales*).

Evolutionary trend Eucommio-cercidiphyllineae (Fig. 5).

The relations of the members *Eucommio-cercidiphyllineae* have been briefly outlined and given reasons for in the previous section. It has to be noted that, of all the just-mentioned trends, they show perhaps most convergences and analogies to some dicotyledonous types with homogenous flowers, which also became arrested on the second evolutionary stage, especially to the order *Hamamelidales*. This suggests that their actual affinities have to be looked for in this direction. The real phylogenetic relations, however, doubtlessly point to the neighbourhood of the evolutionary trend *Trochodendrineae*.

Evolutionary trend Amentiferineae (Fig. 5).

The members of the evolutionary trend *Amentiferineae*, whose mutual relations have also been dealt with in the previous section, represent, as a matter of fact, only a set of amentiferous derivatives, to a certain degree related to the evolutionary trend of the genera *Cercidiphyllum* and *Eucommia*, which themselves are already strongly affected by floral reductions; in a sense, the *Cercidiphyllum* itself is, moreover, of an amentiferous nature. In the whole trend we have been able to distinguish the following three fundamental evolutionary lines: 1. the *Fagoideae* (orders *Fagales* and *Balanopsidales*) with predominantly mesotrophic types, for the most part adapted to conditions of the temperate zones where they formed secondary centres of their geographic distribution, 2. *Myricoideae* (order *Myricales*) also with predominating mesotrophic types, but of thermophilous character, 3. *Verticilloideae* (order *Casuarinales*) representing a typically xeromorphous branch. The evolutionary line of the *Casuarinales* is evidently nearer to that of the *Myricoideae* than to the *Fagoideae*.

Evolutionary trend Urtico-platanineae (Fig. 5).

The third trend *Urtico-platanineae* includes, besides the order *Rhoipteleales*, the affinities of which have already been mentioned, also the orders *Platanales* and *Urticales*. In this paper, the family *Platanaceae* is given the status of an independent order *Platanales* whereas most taxonomers place it directly into the order *Hamamelidales*; this assumption

would, to some extent, be in accordance not only with various mutual analogies in pollen-grains (Erdtmann), but also with a strong floral reduction, for which the family *Hamamelidales* shows an obvious tendency. On the other hand, some outstanding features revealing its relations to the order *Urticales* have been pointed out by J. Velenovský: e. g. the general nature of germinating young plants, which, after developing two cotyledons,

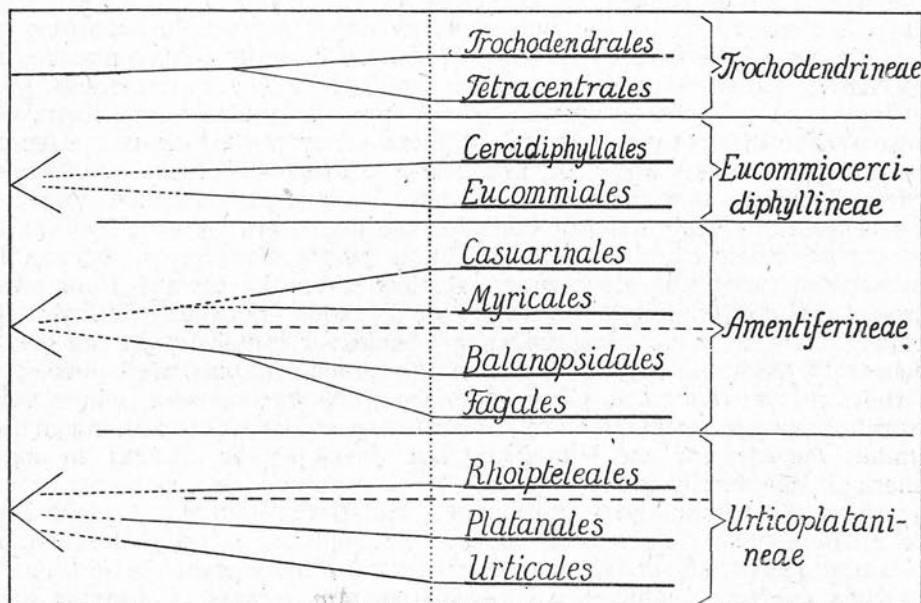


Fig. 5.

Schema rozpadu základních vývojových řad *Trochodendrineae*, *Eucommio-cercidiphyllineae*, *Amentiferineae* a *Urtico-platanineae*.

Scheme of the splitting of the basic evolutionary trends *Trochodendrineae*, *Eucommio-cercidiphyllineae*, *Amentiferineae* and *Urtico-platanineae*.

give, in the course of the whole year, rise only to one leaflet (simple, coarsely toothed in front); at the base of it there is the growing point surrounded by a spathe-like stipule, just as is seen in the young plants of the family *Moraceae*. This, of course, means that a great number of convergences are responsible for various analogies leading the investigators to assign the Platans to the order *Hemamelidales* (notice especially the similarities to the genus *Liquidambar*).

The Platans are an amazingly ancient type. Palaeontologically, they are known to us with certainty from as early a period as the Lower Cretaceous and became quite common already in the Cenomanian. They have also preserved many considerably archaic anatomical features which are more archaic than those found in the relict order *Rhoipteleales*: the Platans do not form any libriform fibres, their vessels are provided with scalariform perforation and their medullary rays are of a heterogenous character. The genus *Rhoiptelea* is already so advanced as to form fibrous tracheides. Both

the genera show more advanced sieve-tubes of the first Hemenway stage; in this respect they are therefore somewhat more progressive than is the trend *Amentiferineae*.

The order *Urticales* itself, the fossil record of some representatives of which dates also from older phases of the Cretaceous (especially the family *Moraceae*), represents in the whole trend the most progressive line which, in some cases was able to give rise to herbaceous elements. Their progressivity is also proved by the nature of pollen-grains which, according to Erdtmann, reveal, with the only exception of some representatives of the family *Ulmaceae*, more complex sculpturings, for the most part 2-6-porate to polyporate (even 15-porate) types. In their original form, the flowers have distinctly epipetalous stamens. They were, however, affected by strong reductions and condensations into dense and massive inflorescences. From the anatomical point of view, too, there is a marked progress. The vessels are very often of considerable diameters (*Morus*, *Ulmus*), in many cases their cross walls have simple perforations (e. g. *Morus*). In herbaceous types the sieve-tubes attained even the second Hemenway stage. On the other hand, the nature of the seed endosperm is inversely proportionate to these progressive tendencies: it is missing in the genus *Rhoiptelea*, very slightly developed in the genus *Platanus*, well developed in the families *Urticaceae*, *Cannabaceae* and *Scyphostegiaceae*, where very often herbaceous derivatives are concerned, it is altogether missing in the families *Barbeyaceae* and *Ulmaceae*, but developed or missing in some genera of the family *Moraceae*.

Upon the whole, the evolutionary trend *Urtico-platanineae* falls into the following two fundamental courses of evolution: 1. the orders *Platanales* and *Rhoipteleales*; the former represents a more archaic evolutionary line than the latter, which again reveals certain features in common with the group *Amentiferae* and the order *Urticales* (particularly the family *Ulmaceae*), 2. a little more progressive order *Urticales*, part of which has still retained its full vigour.

3. Evolutionary trends which attained the third stage.

The third group, i. e. types which reached the third evolutionary stage, includes the whole centrospermous trend (*Centrosperminae*) and that of geraniaceous and buckthorn-like plants (*Geranio-rhamnineae*). The reasons for this classification is, first of all, a marked obdiplostemonous floral structure (or epipetalous position of stamens) and then some other phenomena which have led many supporters of the new morphology to the idea of their being of a stachyosporous nature (this especially applies to Centrosperms). The progressivity of both these evolutionary trends, when compared with the preceding ones, lies in the much more pronounced phylloidization of floral members (large bright perianth leaves), in a great number of herbaceous derivatives (which in some groups prevail over woody plants), in the complicated arrangement of ovaries, in their relatively very progressive anatomical structure of vascular bundles, etc. Finally, in some groups (especially with centrospermous types) there are some marked tendencies towards sympetaly.

Evolutionary trend Centrospermineae (Fig. 6).

Often, especially at first sight, the members of the evolutionary trend *Centrospermineae* show various similarities and analogies to the orders *Rosales*, *Saxifragales*, *Rhoeadales* and *Parietales*, sometimes also to some members of the order *Urticales*. As regards the organization of the sieve-

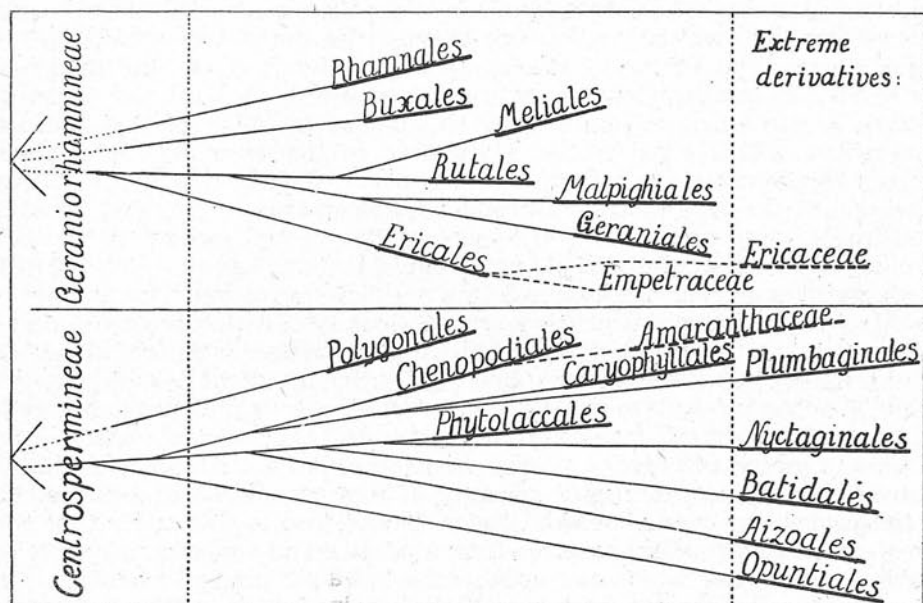


Fig. 6.

Schema rozpadu základních vývojových řad *Centrospermineae* a *Geranio-rhamnineae*.

Scheme of the splitting of the basic evolutionary trends *Centrospermineae* and *Geranio-rhamnineae*.

tubes, they attained for the most part the second Hemenway stage, some (particularly herbaceous types) even the third, i. e., their progress was relatively greater than that achieved by the trend *Urtico-platanineae*. Two parallel fundamental evolutionary courses stand out clearly in this case. The first course (*Polygonoideae*) is represented by the only order *Polygonales* with tiny florets and markedly developed sheaths at the base of the petioles, the second (*Chenopodio-caryophylloideae*) comprises all the rest of centrospermous types. Their mutual relations, although considerably remote from the morphological point of view, are, according to Erdtmann, more clearly indicated by some common features in the pollen-grain sculpturings. The second evolutionary course *Chaenopodio-caryophylloideae*, splits distinctly into two lines. One of them, i. e. the proper chenopodio-caryophylloid line (in a strict sense) has preserved in its flowers a very consistent obdiplostemony (or at least stamens which due to reductions became epipetalous). It includes one series with tiny flowers, convergent

to the order *Polygonales*, i. e., the *Chenopodiales* (with a rather marked tendency towards halophily, xeromorphous specialization and sympetaly; it comprises an upon the whole sympetalous derivative *Amarantaceae*) and a series with large flowers, the order *Caryophyllales*, which more or less shows a tendency towards hygrophily. The order *Plumbaginales* is to be considered as a sympetalous derivative of this last evolutionary line, especially because of a great similarity in pollen-grains (Erdtmann). The second line, which can be characterized as the phytolaccoid line, is rather more disposed to lose the epipetalous stamen ring. This tendency has given rise to flowers where stamens alternate with petals (or perianth leaves). It is the order *Phytolaccales* that forms the basis of this line. Its members reveal a considerable fluctuation in the arrangement of their flowers (flowers are both acyclic and cyclic, stamens obdiplostemonous or, if one of the two whorls was reduced, epipetalous, or alternating with perianth leaves; moreover, some genera have even apocarpous ovaries [*Ercilla*, *Anisomeria*, the sub-genus *Pircunia* from the genus *Phytolacca*]). As derivatives of the phytolaccoid line we can regard the family *Nyctaginaceae* (*Mirabilaceae*), which is a sympetalous type with a whorl of alternating stamens, very probably the amentiferous order *Batidales*, also with an alternating whorl of stamens, and finally the succulent xerophytes, the family *Aizoaceae* (*Mesembryanthemaceae*). As a very old succulent xerophytic derivative (rare fossil record goes as far back as the Eocene), the cactaceous order *Opuntiales* is also to be placed here. Its true relations have been very indistinct until recently. It was considered as being allied to the parietal or even rhoeadoid types. It was just to this order that the above-mentioned family *Aizoaceae* took a parallel and convergent course of development (general external appearance, multiplication of stamens). On the other hand, certain important differences can be found between them: the endosperm has been preserved in the *Aizoaceae*, but lost in the order *Opuntiales*. The *Opuntiales* reveal strong tendencies towards floral zygomorphy. Mutual relations among all the mentioned groups are confirmed by a very similar nature of pollen-grains (Erdtmann) which disagree with any other opinion as to their affinities; this is of special importance in evaluating the relations of the *Opuntiales* and the *Batidales*.

Evolutionary trend Geranio-rhamnineae (Fig. 6).

At first sight, the members of the evolutionary trend, called in this paper *Geranio-rhamnineae*, have much in common with a great number of columniferous representatives belonging to the orders *Euphorbiales*, *Celastrales*, and *Sapindales*. The similarities among them being based not only on morphological, but also on biochemical characteristics, closer relations have been suggested. As in the preceding trend, a marked obdiplostemony or epipetalous position of the stamens (more rarely an alternating position, due to the reduction of an obdiplostemonous one, e. g. in the genus *Linum*) excludes the assumption of too close or direct affinities. Just as the foregoing trend also this trend of *Geranio-rhamnineae* reveals a considerable degree of progressivity in the general morphological arrangement of the flowers as well as in a great number of anatomical features: many representatives have vessels of considerable

diameters, many woody plants often have sieve-tubes of the second Hemenway stage. In the whole trend we can easily distinguish three considerably independent lines, the mutual relation of which can today hardly be more accurately ascertained. Also the nature of pollen differs in each of them. According to the outstanding orders, following names can be given to these lines: *Geranio-rutoideae*, *Buxoideae* and *Rhamnoideae*. As to the pollen sculpturings, Erdtmann's discoveries can hardly enable us to find any closer analogies between the different families belonging here and the other plant groups. All that perhaps may be stated is that the pollen of the rhus type (i. e. grains considerably similar to the pollen found in some representatives of the family *Anacardiaceae*) predominates in the geranio-rutoid evolutionary line (orders *Geraniales*, *Malpighiales*, *Rutales*, *Meliales*), whereas the crotonoid pollen type, known in some members of the family *Euphorbiaceae*, prevails in the family *Buxaceae*. These entirely peculiar types of pollen, however, do not afford any solid basis for determining their true affinities.

In the lines *Geranio-rutoideae* (orders *Geraniales*, *Malpighiales*, *Rutales* and *Meliales*) we can, to a various degree, discover a tendency to the reduction of the endosperm, to the formation of glandular floral discs (with the exception of the proper *Geraniales*) and, in many plants, to floral zygomorphy, to the fusion of stamens as well as to sympetaly (*Simarubaceae*, *Meliaceae*). As regards the origin of the herbaceous element, the following two developmental courses may be pointed out: the one towards the orders *Malpighiales* and *Geraniales* (simultaneously showing a marked convergence to columniferous types) which embraced the majority of herbaceous elements, and the other towards the orders *Rutales* and *Meliales*, where woody types were further on predominantly developing.

The second line *Buxoideae* comprising the only family *Buxaceae* (as the order *Buxales*) was frequently linked up with the order *Euphorbiales* because of certain analogies in the fruits. This assumption having been rejected by J. Velenovský, who considered these analogies as mere convergences, attempts were later made to find some relations to the orders *Celastrales* or *Sapindales* (J. Velenovský, A. Engler, F. A. Novák) and even to the family *Hamamelidaceae* (J. Hutchinson). This assumption, however, disagrees not only with the buxoidean marked epipetaly, which cannot be found in those plants, but also with a different nature of pollen (according to Erdtmann). Unlike the *Geranio-rutoideae*, this line has not developed any glandular floral discs nor reduced the endosperm.

The third evolutionary line *Rhamnoideae*, represented by the only order *Rhamnales* (families *Rhamnaceae* and *Vitaceae*) is characterized by massive glandular discs; the seed endosperm is well preserved. It differs from the preceding plant groups by a quite different arrangement of ovaries.

Palaeontologically, all the three lines are very ancient, because leaf imprints strongly reminding of their representatives can be traced as far back as the Cenomanian, some even until the late phases of the Lower Cretaceous.

To the whole evolutionary trend *Geranio-rhamnineae*, in the neighbourhood of its geranio-rutoid line, which shows so marked tendencies to sympetaly, is assigned in this paper, as its pronouncedly sympetalous derivative, the order *Ericales* together with the family *Empetraceae*. On different grounds (especially because of the nature of stamens and ovaries) this order is suspected by some botanists to be related to guttiferoid types. It is very unfortunate that the determination of these relations cannot be based on the nature of pollen-grains which, according to Erdtmann, have been extremely affected by reductions and are bound in tetrads (quite analogously to the family *Empetraceae*). Some characteristics of this order, e. g. similar general structure of flowers, presence of analogous glandular discs and volatile oils (especially in glandular hairs) as well as positive serodiagnostical reactions with the families *Geraniaceae*, *Rhamnaceae*, *Vitaceae* and even *Celastraceae*, *Sapindaceae* and *Polygalaceae*, however, point to its being related rather to geranio-rhamnoid than to guttiferoid types. The relation of the family *Empetraceae* to the other representatives of the order *Ericales* is, with all probability, similar to the relation of the family *Linaceae* to the representatives of the order *Geraniales* or to that of the families *Nyctaginaceae* and *Batidaceae* to centrospermous plants (of the two whorls of obdiplostemonous stamens the epipetalous one has ceased to exist). The branching off of the whole order *Ericales* must have taken place in very ancient times. Palaeontologically, many of its types may be traced with considerably certainty as far back as the middle phases of the Cretaceous; this agrees with many rather primitive anatomic features preserved by this order: many of its members form no libriform fibres (only tracheides), their vessels bear scalariform or reticulate perforations. Apart from this, however, there are some features showing a marked progressivity: a great number of the genera have sieve-tubes of the second Hemenway stage.

C. Remarks on Eleven Fundamental Evolutionary Trends (incl. two Old Sympetalous Plant Groups) of Dicotyledons with Flowers Assumed to be of Homogenous Nature. (Fig. 7.—13.)

Most plant groups discussed in the preceding section [B] gave a good deal of trouble to systematists setting up a single rather large genealogical tree to illustrate the development of Angiosperms. On the contrary to this, the groups included in the eleven fundamental evolutionary trends with assumed homogenous flowers offered on the whole no difficulties when even complicated pedigrees were devised. As has already been stated, this striking difference is only apparent and is perhaps mostly based on the general, more relict nature of the plants which are supposed to have heterogenous flowers. Their relict nature may also be in connection with the fact that the first series of evolutionary trends (i. e. with heterogenous flowers) predominantly contains evolutionary trends of a more archaic nature, arrested on the first or the second developmental stage, whereas the second series of evolutionary trends (i. e. trends with homo-

genous flowers) is represented mostly by trends that reached the third most progressive evolutionary stage.

Plant types, arrested on the first evolutionary stage form the only one evolutionary trend *Polycarpiceae*. The types, arrested on the second developmental stage are divided into four, upon the whole independent evolutionary trends of a considerably relict character, i. e. the *Dilleniineae*, *Canellineae*, *Hamamelidineae* and *Rhoeadineae*. Finally, extremely numerous types reaching the third developmental stage together with their different sympetalous derivatives are classified into the following six rather well-defined evolutionary trends: the *Crucifereae*, *Parietaleae*, *Saxifrago-rosineae*, *Columnifero-tricocceae*, *Guttifero-myrtineae* and *Umbellifero-celastrineae*. Apart from these also *Sapoto-primulineae* and *Thymelaeo-proteineae* may be reckoned here; they are two apparently rather polyphyletic lines of ancient sympetalous plants which cannot be easily linked up with any of the mentioned trends. The synopsis of the system, annexed to this paper, shows what these conceptions really mean. Affinities among these great evolutionary trends can objectively be ascertained with as little probability as can be those among the trends with heterogenous flowers. It is perhaps between the trend *Rhoeadineae* and the more progressive *Crucifereae* as well as between the order *Pittosporales* and the trend *Saxifrago-rosineae* that such relations are more apparent; for this reason these two pairs of trends are very often by various botanists classified even as common orders.

1. Evolutionary trends arrested on the first stage: *The evolutionary trend Polycarpiceae* (see Fig. 7).

The most archaic evolutionary trend *Polycarpiceae* is very often referred to as a single large order *Ranales* (or *Polycarpales* or else *Ranunculales*). The more was it studied in detail, the more did appear the amazing variety in its forms. Besides a great number of pronounced relicts, it embraces groups manifesting their full vigour even today and forming a number of herbaceous elements as well as derivatives both aquatic and amentiferous. Due to this fact, many botanists divide it into a great number of independent orders, e. g. Hutchinson into the following five orders: *Magnoliales*, *Annonales*, *Laurales*, *Ranales* and *Berberidales*. It was not until some very detailed monographies (J. W. Bailey, Ch. G. Nast, B. G. Swamy, A. C. Smith, P. Ozenda) and Erdtmann's palynological studies were published that this variety of forms and the part played by convergences in the development of the whole trend have been revealed in their true light (e. g. the double nature of plants belonging to the present-day family *Nymphaeaceae*). The antiquity of the whole trend is apparent from a great number of primitive morphological (leaf-like and three-veined type of the stamens, apocarpous gynoecia, open ovaries, imperfect stigmas, lack of styles), as well as anatomical (homoxylous wood, very primitive sieve-tubes of the first Hemenway stage, primitive vessels with scalariform perforations, etc.), features which are commonly known and to different degrees developed in different genera. Some, especially anatomical, features, however, indicate certain progressivity within the first developmental stage on which these types became arrested, e. g. simple vessel perforation found

in the family *Magnoliaceae*, sieve-tubes of the second Hemenway stage in many herbaceous orders, stabilization of the floral diagram with a small number of members in the families *Lauraceae* or *Berberidaceae*, formation of sympetalous derivatives (*Myristicaceae*, *Aristolochiaceae*). The nature of pollen-grains clearly indicates two main courses of evolution, one basically monosulcate, the other tricolpate. These courses, as may be judged from

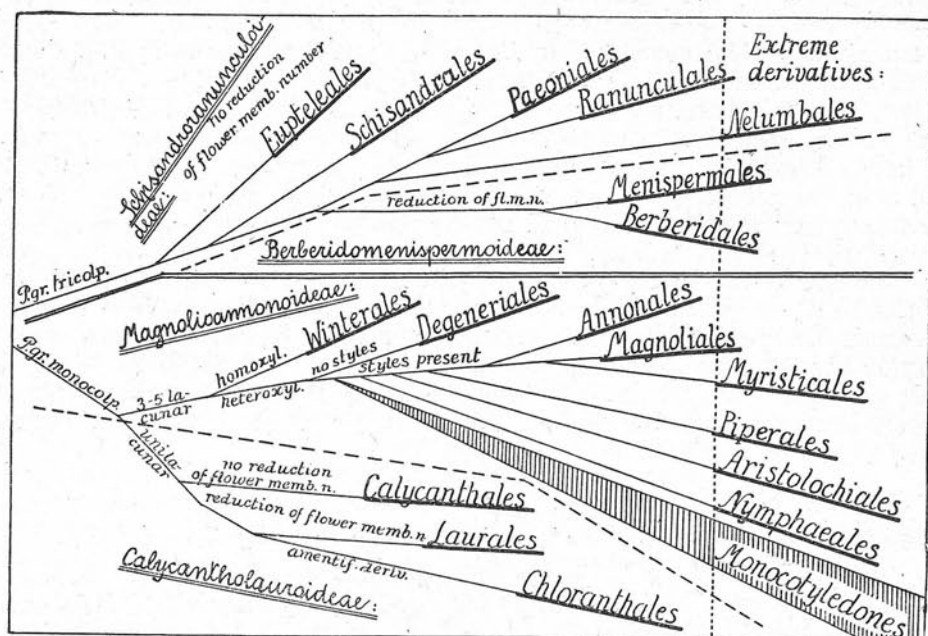


Fig. 7.

Schema rozpadu základní vývojové řady *Polycarpiceae* s naznačením vztahu k rostlinám jednoděložným.

Schema of the splitting of the basic evolutionary trend *Polycarpiceae* with indicated relation to the Monocotyledons.

some outstanding anatomic features (e. g. anatomy of stem nodes) split further into some developmental lines from which different considerably specialized derivatives (aquatic, amentiferous, sympetalous) branched off. According to such criteria and the nature of flowers, as shown in annexed tables (see also the synopsis at the end of this paper) and in accordance with the individual above-mentioned evolutionary trends, not so few as five, but twenty groups, independent to such a degree as to represent valid orders, can be distinguished in the whole trend *Polycarpiceae*. These again can be grouped into four fundamental evolutionary lines:

The *Magnolio-annonoidae* embracing the orders *Degeneriales*, *Winterales*, *Magnoliales*, *Annonales*, sympetalous derivatives *Myristicales* and *Aristolochiales* (with the parasitic families *Rafflesiaceae* and *Hydnoraceae*), amentiferous derivatives *Piperales* and *Hydrostachyales*, aquatic derivatives *Nymphaeales* (the *Nelumbaceae* excepted!) and *Ceratophyllales*.

The *Callicantho-lauroidae* including the orders *Callicathales*, *Laurales*, and the amentiferous derivative *Chloranthales*.

The *Schizandro-ranunculoideae* with the orders *Eupteleales*, *Schizandraceae*, *Paeoniales*, *Ranunculales* and the aquatic derivative *Nelumbales*.

The *Berberido-menispermoideae* with the orders *Berberidales* and *Menispermiales*.

Fossil record of many members of this whole evolutionary trend (of course, regardless of the majority of herbaceous derivatives) and many of its extreme derivatives (e. g. aquatic derivatives) date already from the late phases of the Lower Cretaceous. At more places their pollen was ascertained even in the Lower or the Middle Jurassic (e. g. the pollen quite similar to that of the representatives of the families *Magnoliaceae*, *Nymphaeaceae* and *Nelumbaceae*).

2. Evolutionary trends arrested on the second stage: *Dilleniineae*, *Canellineae*, *Hamamelidinae* and *Rhoeadinae*.

The relatively isolated orders *Dilleniales*, *Pittosporales*, *Coriariales*, *Canellales*, *Hamamelidales*, and *Rhoadales* show a substantially more advanced organization and are therefore to be regarded as belonging to the second developmental stage. As is admitted in almost all taxonomic compendia, they reveal, in a primitive state, many features which can be found fully developed in various much more advanced orders. One of them, the order *Canellales*, has a monosulcate pollen, all the others a pollen more or less derived from the tricolpate type.

Various genera of the orders *Dilleniales*, *Pittosporales*, and *Coriariales*, which are here united in the evolutionary trend *Dilleniineae*, disclose many features in common with the orders grouped in this paper into considerably progressive evolutionary trends *Saxifrago-rosineae*, *Guttifero-myrtineae*, and *Umbellifero-celastrineae* and perhaps also *Parietaleae*. Many botanists, after all, assign them therefore to some orders of these trends as their most primitive members (and give them the status of orders or only families: they connect the *Coriariaceae* with the order *Celastrales*, the *Pittosporaceae* with the order *Rosales*, the *Dilleniaceae* with the order *Guttiferales* or classify them as independent orders). It is sure that the orders *Pittosporales* and *Coriariales* are of a somewhat more progressive character than is the order *Dilleniales*; this is also indicated by the nature of their pollen-grains, as ascertained by Erdtmann. In the order *Dilleniales* the pollen is still of about the same primitive nature as are the tricolpate pollen-grains in the evolutionary trend *Polycarpiceae*. On the other hand, the pollen of the orders *Coriariales* and *Pittosporales* reveals substantially more derived shapes, but, according to Erdtmann, no closer analogies to that of the orders *Celastrales* or *Rosales* can be found. For this reason they are to be regarded as entirely independent orders and placed into one evolutionary trend *Dilleniineae*.

The order *Canellales* is often classified as a very primitive family *Canellaceae* of the parietal order *Bixales* because of the morphological arrangement of its ovaries. Some more recent botanists, however, due to its monosulcate pollen type, link it up rather closely with the magnolio-annonoid line of the trend *Polycarpiceae*. It may be assumed that in both

cases some of its either archaic or progressive features have been overestimated. Certain convergent tendencies to the parietal types cannot be denied, but the nature of the pollen indisputably indicates the individual character of this order. Its archaity manifests itself also in some anatomical features (e. g. instead of libriform fibres which are missing, the wood has only tracheides). It is indisputably a type of a very relict nature with no apparent closer relation to other evolutionary trends. For this reason, it may be considered as a representative of the independent evolutionary trend *Cannelineae*, also reaching the second stage of evolution.

The order *Hamamelidales* shows many morphological analogies both with the members of the order *Rosales* and with those of the amentiferous trend (in a strict sense). To some extent, it recalls the last-named plants by the structure of its wood, but it differs from them very distinctly in the normally alternating stamens. In spite of this, these three groups are often considered as being phylogenetically interrelated. It has, however, been clearly shown by Erdtmann's palynological discoveries that such relations cannot be looked for in neither direction because of the absence of necessary common features in a more delicate morphology of pollen-grains. Various analogies with the group *Amentiferineae* are mostly based on the kind of floral reductions. The same kind of reductions occurs, however, also in the families *Eucommiaceae* or *Platanaceae* (analogy to the genus *Liquidambar*). It seems that no actual affinities, but mere convergences can be considered in all these three cases. Palaeontologically the order *Hamamelidales* appears to be very ancient. Some fossil records date from as early as the North American Cenomanian. In the middle phase of the Tertiary many of its genera became widely distributed all over the Northern Hemisphere. In view of all these circumstances this order is to be regarded as a further fundamental line of evolution, i. e. as the evolutionary trend *Hamamelidinae*. The family *Balsamifluae* (together with the genus *Liquidambar*) and the amentiferous type *Myrothamnaceae* could be considered as some extreme reductional derivatives belonging to this trend.

The order *Rhoeadales* is taken here in the narrower Hutchinson's sense, i. e. without the substantially more advanced families *Capparidaceae*, *Cruciferae* (or *Brassicaceae*) and their relatives. This narrower definition of the order is supported by Erdtmann's palynological discoveries which point to substantially great differences found in the pollen of the families *Capparidaceae* and *Cruciferae* when compared with that of the order *Rhoeadales* in a strict sense. The pollen of this order bears rather more resemblance to the more primitive pollens of some groups of the trend *Polycarpiceae* (*Berberidaceae*, *Ranunculaceae*). Besides, as regards the morphological character, various analogies can be found not only towards the families *Capparidaceae* and *Cruciferae*, but also towards some parietal types. Here again, just as was seen in all the above-mentioned orders, there is another case of a not clearly defined plant group, even if analogies with morphological (and some biochemical) features of the families *Capparidaceae* and *Cruciferae* are perhaps more clearly pronounced. As it represents a considerably individual evolutionary trend, it is given here the name *Rhoeadinae*. With them, as a direct specialized derivative is linked up the insectivorous family *Sarraceniaceae* which, together with the families

Droseraceae and *Nepenthaceae*, is usually placed into the common order *Sarraceniales*. This opinion is supported by the nature of the pollen (Erdtmann) and by some morphological features known long ago (A. L. Jussieu, 1789), e. g. the character of the stigma and stamens. The pollen of this family entirely differs from that of the families which are usually connected with it; it has common features with the pollen of the representatives of the order *Rhoeadales* in the strict Hutchinson's sense (and is therefore more closely related to this order than to the families *Capparidaceae* or *Cruciferae*). Mutual analogies are to be interpreted again by mere convergences resulting from a similar (insectivorous) habit.

3. Evolutionary trends which attained the third stage.

Very complicated conditions can be traced in the evolutionary trends which reached the third developmental stage. In the following paragraphs reasons for this classification will be given as well as some light will be thrown on phylogenetic relations assumed to exist among the different orders.

Evolutionary trend *Cruciferineae* (Fig. 8).

Mutual relations of the orders *Capparidales* and *Cruciferales*, assigned to this trend are rather clear. Also as regards the similarity of the pollen, these orders are nearer to each other than to the order *Rhoeadales* (in a strict sense). They both represent the final stage of two obviously divergent, though closely related, lines of evolution, one of which (the *Capparidales*) has prevalently preserved woody character as well as many more archaic morphological features, whereas the other (the *Cruciferales*) represents a much more progressive element; it gave rise to innumerable herbaceous species considerably distributed even over colder areas and containing also a great number of elements adapted to strongly xerophilous or hygrophilous life. Besides, its simple floral diagram became more stable. As has already been said, this whole trend has many features in common with the more primitive order *Rhoeadales*. Actual affinities, however, are to be regarded as very remote: it is rather the parallelism and convergences that played a much more important part in their development, in the course of which one line (the *Rhoeadineae*) became arrested in its evolution much earlier than the other (the *Cruciferineae*).

Evolutionary trend *Parietaleae* (Fig. 8).

As all morphological as well as serodagnostic studies have shown so far, the evolutionary trend *Parietaleae* does not seem to represent any simple evolutionary series. Most probably it consists of at least two parallel evolutionary lines which are convergent to each other. Besides, Erdtmann's palynological discoveries reveal that these two lines may not be enough homogenous. For the most part, even within the orders, as they are defined by systematic botanists, the pollen is not of a sufficiently uniform nature. In addition to it, it will be necessary to solve the problem whether the group is really of a polyphyletic character or whether the orders included into it are only of an eurypalinous nature. One of the two

fundamental lines (the dillenioid evolutionary line) embraces the orders *Bixales*, *Tamaricales*, *Passiflorales*, i. e. orders whose members, by some of their features, betray relations to the evolutionary trend *Dilleniineae*, and particularly to the order *Dilleniales*; these relations may be due either to a very remote relationship, or to a parallelism in development. The second line (the rhoeadoid line) includes the orders which

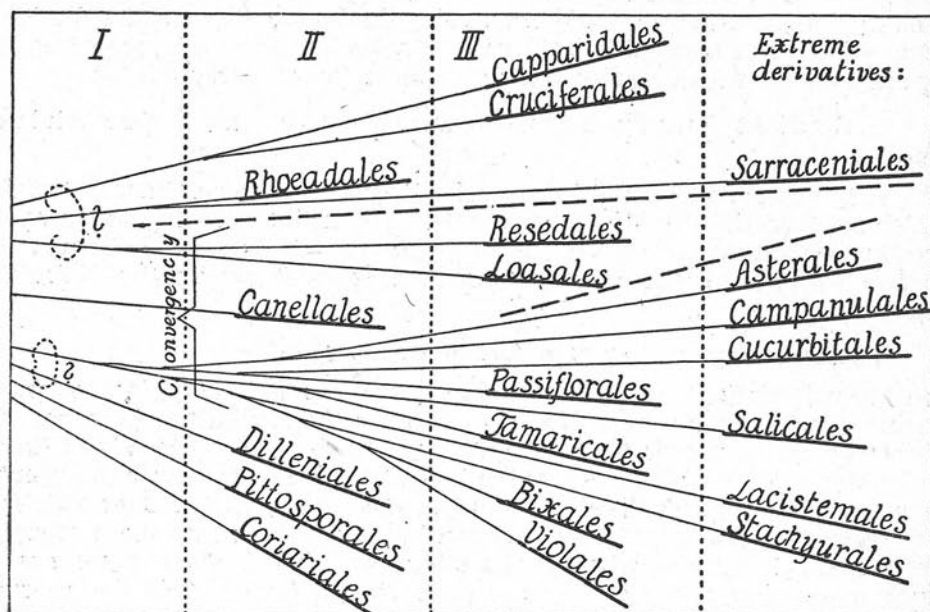


Fig. 8.

Schema rozpadu základních vývojových řad *Parietaleae*, *Cruciferineae* a *Rhoeadineae*.

Scheme of the splitting of the basic evolutionary trends *Parietaleae*, *Cruciferineae* and *Rhoeadineae*.

show some common features with the more primitive evolutionary trend *Rhoeadineae*. It is the order *Violales* (together with the family *Resedaceae*, often considered as belonging to this line) and *Loasales* in Hutchinson's sense which could be considered here.

Although from the morphological point of view the individual members of the dillenioid series do not offer any more difficult problems as to their relations (see J. Hutchinson, F. A. Novák) Erdtmann's palynological researches indicate that there may be some differences. The most uniform kind of pollen is found in the order *Passiflorales*. It bears a striking resemblance to the pollen of the very progressive sympetalous orders *Cucurbitales* and *Campanulales*. This fact clearly proves that, in spite of all morphological and serodiagnostic uncertainties, both these orders are sympetalous derivatives belonging to the dillenioid series of the parietal trend. The order *Cucurbitales* developed a tendency towards reducing the

endosperm (which is abundant only in the family *Caricaceae*; this family also still has a superior ovary and for this reason it is by some systematists reckoned among the parietal types) but preserved a double integument, whereas the order *Campanulales*, while preserving the seed endosperm, tended to simplify ovules to formations with a single integument.

The *Compositales* (or *Asterales*), an extremely progressive and for the most part herbaceous order, can with great probability be considered here as a further sympetalous derivative. Some features found in this order strongly remind of the order *Campanulales* (ovules provided with a single integument, inulin instead of starch, latex tubes, morphology of inflorescence). But even here we find some substantial differences, e. g., according to B l o g o v ě š ě n s k ý, a different mode of breathing. As regards pollen-grains, E r d t m a n n detected a far greater number of analogies between the pollen of the family *Compositae* and that of the families *Umbelliferae*, *Brunoniaceae*, *Goodeniaceae* and *Calyceraceae*, than between the pollen of the family *Compositae* and that of the family *Campanulaceae*. All that, of course, does not offer any final univocal solution, but does not disagree with the relations to the order *Campanulales*. So far, in spite of occasionally occurring opinions that the compositean type might be related to umbelliferous plants, most botanists have (and most likely with full right) in this case considered the relations to the order *Campanulales* as much more natural. The *Compositae* are most probably a very young type, because they are known to us with certainty from as late as the older phases of the Tertiary. They have developed an immense number of very progressive herbaceous types, revealing even today an extraordinary plasticity with regard to various ecologic conditions, and did not reach the maximum development until the late Cainozoic and the present time. Their progressivity, relatively greater than that of both the preceding sympetalous orders, is evident not only from a greater condensation of flowers into dense head-like inflorescences (where individual flowers, according to their position, very frequently underwent quite a special kind of adaptation; there is a certain degree of convergence to the conditions present in umbel inflorescences of some umbelliferous types) than can be found in the order *Campanulales*, but also from the loss of the seed endosperm. Also from the anatomical point of view they have, for the most part, reached the highest (third Hemenway) stage in the organization of the sieve-tubes. All this is in agreement with the complexity and variety of pollen-grains (a characteristically eurypalynous group!) which, of course, decreases the importance of pollen for solving the problem of affinities. Here the pollen may indicate only relatively close relations between the family *Compositae* and the small group *Calyceraceae*, sometimes included into the order *Rubiales* (into the neighbourhood of the family *Dipsacaceae* with which they share the same kind of a simple stigma, but from which they substantially differ in the nature of pollen). Apparently, this is a case of a member of the order *Compositales* (*Asterales*), rather less progressive than are the proper *Compositae* (it still has a developed endosperm and its pollen bears simpler sculpturings; from the *Compositae* it also differs in having a simple stigma). On these grounds and in agreement with most systematic botanists the

group *Compositales* (the family *Calyceraceae* included) is to be regarded as a further and youngest sympetalous derivative of the parietal trend which, in addition to the general floral reduction and condensation, underwent a strong reduction of the ovaries (fruit: one-seeded achene).

As far as sympetalous derivatives of the parietal evolutionary trend are concerned, three more or less parallel lines of evolution can be distinguished; they branched off successively and are not directly interrelated. Each of them attained a different degree of developmental progressivity. The highest stage of evolution was indisputably reached by the order *Compositales* (*Asterales*).

With the dillenioid evolutionary series, as its amentiferous derivatives are linked up the family *Lacisternaceae*, the whole order *Salicales* as well as the family *Stachyuraceae* (see the section dealing with amentiferous types).

Considerably intricate are the conditions in the second, i. e. rhoeadoid evolutionary series, which is of a rather doubtful character. The families *Violaceae* and *Resedaceae*, so far usually included into the order *Violales* have, in the light of the most recent researches, revealed very different characters both from morphological (F. A. Novák) and palynological points of view. Only the pollen of the family *Resedaceae* resembles that of the family *Capparidaceae* and *Tovariaceae* (but not that of the *Cruciferae*!). Unlike the *Violaceae*, the *Resedaceae* disclose positive serodiagnostic reactions with the family *Capparidaceae*. Germinating plantlets of the family *Violaceae* remind of those of the family *Cistaceae*. Also in the order *Loasales*, taken in the so far current sense (*Turneraceae* and *Loasaceae*), there are similar incongruities. According to Erdtmann, the pollen of the family *Turneraceae* is, to a certain degree, analogous to that of the *Passifloraceae*. Besides, a closer relationship of these two families has been suggested by F. A. Novák also because of morphological reasons. As Erdtmann states, the pollen of the family *Loasaceae* does not reveal much, nor does it show closer similarity to the pollen of the trends *Rhoeadineae* or *Cruciferineae*. In these plants, however, a positive serodiagnostic reaction with the families *Capparidaceae* and *Resedaceae* was ascertained. All this signifies that the order *Violales*, the family *Resedaceae* excluded, is to be placed in the dillenioid evolutionary series. In the same way the family *Turneraceae* is to be separated from the order *Loasales* and assigned somewhere near the order *Passiflorales*. The *Resedaceae*, as an independent order *Resedales*, and the order *Loasales* (without the family *Turneraceae*) may perhaps only be considered as members of the rhoeadoid series of the trend *Parietaleae*. From morphological and biochemical points of view some systematic botanists (F. A. Novák) recently solve these problems by assigning the family *Resedaceae* directly to the order *Rhoeadales* (in the broadest sense, under the name *Papaverales*) and by including all the other orders together with the families *Caricaceae* and *Datisceae*, which are most frequently regarded as belonging to the order *Cucurbitales*, into a common order to be called *Cistales* and linked up with the order *Rhoeadales* (in the broadest sense, the *Papaverales*). According to new Erdtmann's discoveries, however, this conception (direct relations to the *Rhoeadales*) does not seem to be sufficiently probable.

The evolutionary trend *Saxifrago-rosineae* (Fig. 9).

This evolutionary trend is more or less clear; it covers, to a great extent, the order *Rosales* in the older, broader sense and reveals two indisputably interrelated evolutionary lines, namely the more original orders *Cunoniales*, *Saxifragales* and *Rosales* (in the narrower Hutchinson's sense)* on one side and the order *Leguminosales*, tending towards an extreme floral zygomorphy, on the other.

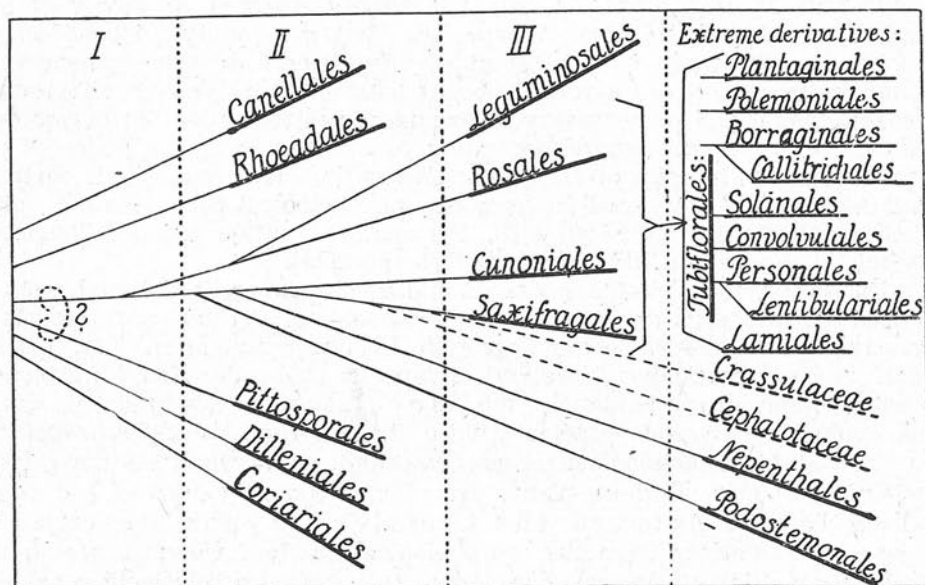


Fig. 9.

Schema rozpadu základní vývojové řady *Saxifrago-rosineae*.

Scheme of the splitting of the basic evolutionary trend *Saxifrago-rosineae*.

In the former line, the floral development proceeds from hypogyny to perigyny and even epigyny. This process is accompanied by the simplification of the floral diagram in different respects and mostly results in normal diplostemony, less frequently in some derived (pseudo-) obdiplostemony (in the families *Saxifragaceae*, *Crassulaceae*, in the genera *Potentilla*, *Rhophiolepis*, *Mespilus*, *Sanguisorba*). The endosperm remained preserved. In the latter line (the order *Leguminosales*) the progression is even more marked, but of a different kind: hypogyny is consistently preserved, there are coalescences, splitting in the androecium and extreme zygomorphy, the number of carpels is reduced to only one, the endosperm lost (the primitive *Caesalpiniaceae* excepted). This double evolutionary tendency is also proved by palynology. As regards both the general shape and more delicate sculpturings of pollen-grains, the orders *Cunoniales*, *Saxifragales*, and *Rosales* show much closer mutual analogies than can be ascertained when these orders are compared with the order *Leguminosales* (Erdtmann).

As the more primitive representatives of the whole trend reveal many characteristics similar to the more progressive members of the trend *Polycarpiceae*, they were, and still in many cases are, derived from such archaic types either directly or through the order *Dilleniales*. Some investigators try to find here some relations to the order *Hamamelidales*. It even happened that some progressive types of the trend *Polycarpiceae* or also *Dilleniaceae*, e. g. the family *Calycanthaceae* (J. Hutchinson) or *Pittosporaceae* (F. A. Novák) were even frequently assigned to this trend. This opinion, however, has not been confirmed in any way by Erdtmann's palynological discoveries. Even the family *Pittosporaceae* which, from the morphological point of view, seems to be very near the *Rosaceae* has a pollen of a very different nature. For palynological reasons it seems that it will be necessary to exclude, from the order *Saxifragaceae*, the family *Grayaceae* where, according to Erdtmann, the pollen is of a rutoid nature. In spite of all these palynological discoveries, it is certain that this evolutionary trend is, from the morphological point of view, very much related to, or parallel with, the more primitive trend *Dilleniaceae* (especially the orders *Dilleniales* and *Pittosporales*).

For purely morphological reasons and as it seems with full right, specialized insectivorous derivatives *Nepenthaceae* and *Droseraceae* (excluded from the order *Sarraceniales* and given in this paper the status of the order *Nepenthales*), aquatic derivative *Podostemonales* (the order *Hydrostachyales* excepted), and all sympetalous tubifloral types are linked up with this evolutionary trend (especially with its line *Cunoniales-Saxifragales-Rosales*). So far, palynological researches cannot prove these relations with certainty, because all these plants are of an extremely derived and specialized character. As regards the tubifloral types, they certainly show a great variety from the morphological point of view; according to Erdtmann's palynological discoveries, they reveal a relatively considerable homogeneity. The only exception are the narrower orders *Lentibulariales* (or *Utriculariales*) and *Plantaginiales*; their pollen (and especially that of the *Plantaginiales*, which is of a very derived nature) is more different from that found in the others. The floral morphology, too, of these orders shows many points of difference; this led some botanists to consider the possibility of relating the family *Plantaginaceae* to the trend *Centrospermineae* or to the order *Plumbaginales*, and the family *Lentibulariaceae*, to the family *Primulaceae*. The improbability of such opinions has already been proved by J. Velenovský in a purely morphological way. Both the types are, no doubt, of a strongly derived and specialized character, as geophily and hygrophily played a great part in influencing not only a somewhat different formation of flowers but also the type of pollen-grains.

The problem of the nature of the aquatic family *Callitrichaceae*, very differently estimated by taxonomers, is also to be discussed here. This family has often been considered as being related to columniferous types (the order *Euphorbiales*). According to Erdtmann, pollen-grains are very much simplified by reductions. On the other hand, position of the leaves (opposite), fruit resembling a schizocarp of four nutlets, ovules with

a single integument clearly suggest certain relations to the families *Scrophulariaceae* and *Labiatae* (or *Lamiaceae*).

It is clearly to be seen that the sympetalous tubifloral derivatives have, in their further development, given rise to some more specialized and still further derived types, i. e. the families *Plantaginaceae*, *Lentibulariaceae*, and *Callitrichaceae*. Also the parasitic families *Orobanchaceae* and *Cuscutaceae* may be reckoned among them.

From the palaeontological point of view the members of the whole trend *Saxifrago-rosineae* are relatively less known, although fossil record dating from as early as the Cenomanian gives evidence of the presence of its more progressive line Leguminosales. This is apparently in connection with its occurrence in such regions where there was no chance of their entering as fossils into sedimentary series. The whole trend seems to be considerably old. This may not, however, be the case of its tubifloral derivatives, the remains of which are known with certainty only from the tertiary (or at the utmost from the late Cretaceous?); these are apparently considerably young from the geological point of view.

Evolutionary trend *Columnifero-tricocceae* (Fig. 10).

Like the preceding, the evolutionary trend *Columnifero-tricocceae* is of a relatively homogenous character; judging from the general floral morphology, it seems to have split also somewhere from the neighbourhood of, or parallelly to, the more primitive trend *Dilleniineae*. It embraces the orders *Tiliales*, *Malvales* and *Euphorbiales*. Some tropical families with still relatively little simplified floral diagrams, such as the *Scytotetalaceae* or *Gonystylaceae*, perhaps afford a picture of a relatively original prototype of the whole trend, characterized by the ovules being located at angles in the centre of the whole ovary, the partition walls of which coalesce into a common little column (free central placentation).

From morphological, anatomical and palynological (according to Erdtman) points of view, two evolutionary lines stand out clearly; the first is more original and involves the series *Tiliales* and *Malvales*, the second, which is apparently derived from the first, is more progressive and includes the order *Euphorbiales*.

As regards the floral arrangement, the series *Tiliales-Malvales* tended towards the most various complications in the androecium (abortion, splitting, fusion of the stamens) and the gynoecium (multiplication of partition walls, formation of additional partition walls, especially in the more progressive order *Malvales*), but it preserved larger flowers. In the more progressive series *Euphorbiales* the process of evolution was towards the simplification of flowers: ovary becomes stabilized at number three, flowers are reduced to only one sex, the general reduction results in the formation of miniature perianthless florets with only one stamen or one three-chambered ovary, these florets get clustered into inflorescences resembling even simple bisexual florets (cyathium).

Anatomically neither of them reached its ultimate possibilities. Even in herbaceous types the sieve-tubes attained only the second Hemenway stage, the vessels mostly have simply perforated cross walls. Characteristic is here the presence of secretory cells which in the series *Tiliales-Malvales*

contain only mucilages, glucosides, or even alkaloids, in the more progressive series *Euphorbiales* also oils, toxic proteins, caoutchouc substances; moreover, these secretory cells show a tendency towards a far more luxuriant growth.

This double course of development is also apparent from Erdtmann's palynological discoveries. Erdtmann points out certain common features which are especially clearly visible between the *Tiliales* and *Malvales*. As a more advanced type, the order *Malvales* has a pollen of a more derived kind displaying more complex sculpturings. The pollen of the order *Euphorbiales* has much less in common with that of these two orders. Just as in morphological and anatomical features there is a great variety in the sculpturings of pollen-grains. This leads many botanists to assume a polyphyletic origin of the whole order, but it seems more probable that the order is not only of an ancient origin, but that it has so far preserved its plasticity (notice its possibilities of most different ecomorphoses, there are even cactaceous types). Erdtmann's researches, of course, show that, because of an absolutely different character of the pollen, some families so far assigned here will have to be revised from the taxonomical point of view (the family *Elaeocarpaceae* from the order *Tiliales* [no secretory mucilaginous reservoirs!] perhaps with reference to the order *Bixales*; the families *Daphniphyllaceae* and *Dichapetalaceae* from the order *Euphorbiales*). It is also important to mention that the family *Malpighiaceae*, referred by many botanists to the order *Tiliales*, has an entirely different kind of pollen recalling, to a greater degree, the evolutionary line *Geraniorutoideae* of our trend *Geranio-rhamninae*.

The progressivity of the both mentioned evolutionary branches is apparent (more in the order *Malvales* than in the order *Tiliales*) also in the relative abundance of herbaceous types. In spite of all this both the branches have mostly preserved a well-developed seed endosperm.

All the above-mentioned traces of archaic features (sieve-tubes, endosperm) are in harmony with their rather ancient origin. Many impressions show their presence as early as the middle phases of the Cretaceous. They attained a particularly high degree of prosperity in the Upper Cretaceous and older Tertiary.

Evolutionary trend *Guttifero-myrtinae* (Fig. 10).

Some members of the order *Theales* approaches the more primitive trend *Dilleniinae*, certainly even to a greater degree than does the preceding evolutionary trend: many of them have an indefinite great number of floral members, according to Erdtmann, the pollen of the family *Actinidiaceae* bears considerable resemblance to that of the family *Dilleniaceae*. Morphologically and serodagnostically it exhibits also some resemblances with the trend *Saxifrago-rosinae*. Two main more progressive branches are linked with the archaic line *Theales*: 1. the order *Guttiferales* which preserved the superior ovary, but lost the endosperm, and where stamens got fused in various ways, and 2. the pair of orders *Myrtales* and *Lythrales* which showed the tendency towards the loss of endosperm, various complications in the androecium, and a gradual submersion of ovaries. In the order *Lythrales*, too, herbaceous types branched off and vascular bundles became

complex (mostly bicollateral bundles with intraxylary phloem). All this points to a relatively stronger progressivity and derivation of this order, as compared with the proper order *Myrtales*.

Surprising suggestions about the problem of affinities of this whole evolutionary line have been given by Erdtmann's palynological discoveries. First of all, the relatively close relations between the orders

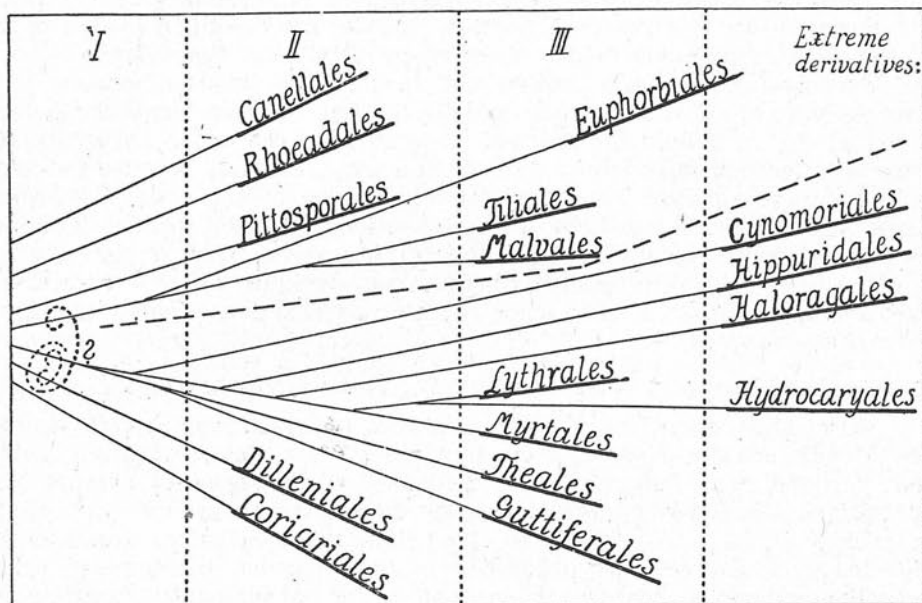


Fig. 10.

Schema rozpadu základních vývojových řad *Columnifero-tricocceae* a *Guttifero-myrtineae*.

Scheme of the splitting of the basic evolutionary trends *Columnifero-tricocceae* and *Guttifero-myrtineae*.

Myrtales and *Lythrales* have been confirmed. Of extreme interest, however, is especially the great similarity of the pollen of the order *Myrtales* (particularly the pollen of the family *Myrtaceae*) to that of the order *Proteales* and then the resemblance of the pollen of the order *Lythrales* (especially the pollen of the family *Rhizophoraceae*) to that of the order *Santalales*. Also the pollen of some families, usually placed into the order *Thymelaeales*, and of the family *Elaeagnaceae* have been found by Erdtmann to be similar in certain respects to that of some members of the series *Myrtales-Lythrales*. All this casts some light on the affinities of the order *Proteales* which has until now been rather mysterious (for more details see the paragraph dealing with the evolutionary trend *Thymelaeo-proteineae*).

The majority of taxonomers link with the order *Lythrales* (particularly near the family *Onagraceae* [or *Oenotheraceae*]) the family *Thelygoniaceae* (strongly derived herbs, the ovules of which are provided with a single integument), aquatic derivatives *Hydrocaryaceae* (or *Trapaceae*), *Gunnera-*

ceae, *Haloragaceae* and *Hippuridaceae*, as well as the parasitic derivative *Cynomoriaceae* (convergent to a certain degree to the order *Balanophorales*). This assumption seems to be fully justified, although, for the time being, there are, apart from the morphological evidence, upon the whole no other reasons for it. Palynology is of no more use here than in the cases where strongly reduced types are concerned. Erdtmann was able to discover only that the pollen of the family *Haloragaceae* resembles that of the *Gunneraceae* (for this reason these two families are classified in this paper as the order *Haloragales*). In other respects all the types seem to be considerably far from one another and to have the status of orders. It is commonly accepted that morphologically the family *Hydrocaryaceae* (which is related to the family *Onagraceae*) is nearest to the order *Lythrales*. All these relations, however, may date from a very far past, because the seed endosperm disappeared to a considerable degree in the order *Lythrales*, but is still very well preserved in the mentioned derived groups. The fact is that palaeontologically many types of the trend *Guttifero-myrtineae* belong to the oldest Cretaceous Angiosperms we know of. It is of interest that the same applies also to some of their aquatic derivatives (*Haloragaceae*, *Hippuridaceae*).

Evolutionary trend *Umbellifero-celastrineae* (Fig. 11).

This trend comprising the choripetalous orders *Umbelliflorales* (families *Alangiaceae* and *Nyssaceae* included), *Pandales*, *Celastrales*, *Sapindales* and perhaps also *Polygalales*, as well as a whole series of sympetalous derivatives seems to represent a series evolutionary parallel (or perhaps at ancient times also related) to the primitive evolutionary trend *Dilleniineae*, particularly to the order *Coriariales*. Because of some morphologically analogous features this last order is by many investigators assigned directly to the order *Celastrales* (e. g. F. A. Novák). According to Erdtmann, however, its pollen is of a much more archaic nature, too different not only from that found in various families of the order *Celastrales*, but also from that discovered in the families of the order *Sapindales*. The whole trend (even irrespective of specialized derivatives) is distinguished by considerably stabilized and simplified floral diagrams, the presence of glandular discs in the flowers, a tendency towards opposite leaf arrangement on the axes, and, from the biochemical point of view, by the presence of volatile oils, resin secretions, tannins and alkaloids (latex tubes producing rubber substances in some sympetalous derivatives; the *Apocynales*). There are obvious tendencies towards the submersion of ovaries, the loss of endosperm, sympetaly, simplifications of ovules to single-integument types, and a general floral reduction.

As far as normal, not derived, and mostly choripetalous orders are concerned, two fundamental evolutionary lines can be distinguished according to what degree the just-mentioned features became developed: 1. the first is represented by the order *Umbelliflorales* (the umbellifloroid line), 2. the second, by the orders *Celastrales* and *Sapindales* (the celastro-sapindoid line) to which the rather isolated order *Pandales* is remotely related. The splitting of the whole trend into these evolutionary lines must have taken place at some time long ago, for the impressions

pointing to the types of both these lines are represented in fact already among the oldest Cretaceous Angiosperms. The separation of the orders *Celastrales* and *Sapindales* is of a little later date, because fossils, suggesting with more certainty the representatives of the order *Sapindales* became more abundant only in the late phase of the Cretaceous.

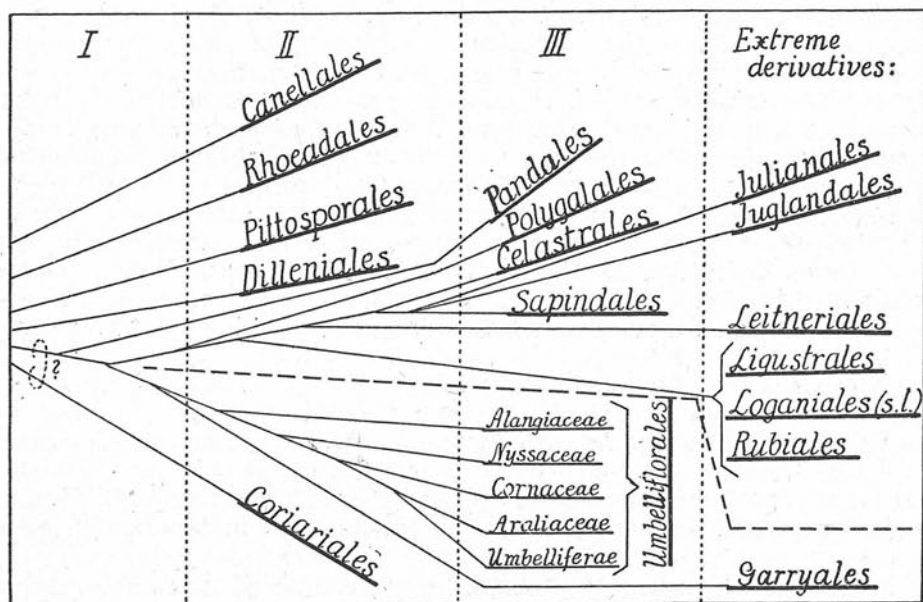


Fig. 11.

Schema rozpadu základní vývojové řady *Umbellifero-celastrineae*.
 Scheme of the splitting of the basic evolutionary trend *Umbellifero-celastrineae*.

Evolutionary tendencies of the mentioned lines are very typical. The umbellifloroid line shows a marked tendency towards the formation of characteristic umbelliform inflorescences; its herbaceous derivatives tend to develop conspicuously broad petioles and multilacunary nodes. As to the celastro-sapindoid line the mentioned splitting resulted on one hand (the order *Celastrales*) in preserving some more original features (endosperm) with an obvious tendency towards sympetaly (*Icacinaceae*, *Stackhousiaceae*, *Salvadoraceae*) and reduction of integuments to only one (*Icacinaceae*, *Aquifoliaceae*), on the other hand (the order *Sapindales*) in the general reduction of flowers, their crowding into dense inflorescences and the loss of endosperm.

Many new suggestions concerning the affinity problem of the plants included into, or related to, this trend, have been made by Erdtmann. As regards the arrangement of pollen-grains, he found that there is a far greater variety within the order *Celastrales* than in the order *Sapindales*; this, in a sense supports the view that the *Sapindales* are of a derived character. In addition to this, Erdtmann's studies confirmed a relative

isolation of the family *Pandaceae*, which is to be considered as some lateral evolutionary branch of the series *Celastrales-Sapindales*. It has been further proved that the family *Staphyleaceae* belongs to the order *Celastrales* (as already suggested by F. A. Novák) and not to the order *Sapindales* to which it was often assigned. The pollen of the family *Connaraceae*, so far usually placed into the order *Celastrales*, was found to be of an entirely different nature, rather recalling that of the order *Rosales* (to which this family was assigned by F. A. Novák for morphological reasons). The family *Didiereaceae* too, greatly differs in the pollen arrangement from the other representatives of the order *Sapindales*; this, as can easily be seen, is due to its being a strongly xeromorphous derived type. Also the families *Sabiaceae*, *Empetraceae* and *Corynocarpaceae* have pollen grains of a substantially different nature. In the case of the family *Sabiaceae*, the problem of its pollen has not been definitely solved and a further revision is desirable. The family *Empetraceae*, owing to the fact that it has a pollen quite analogous to that of the family *Ericaceae*, is to be placed into the order *Ericales*. Finally, the family *Corynocarpaceae* has to be assigned to the trend *Guttifero-myrtineae*, because its pollen bears a striking resemblance to that of some members of this trend.

With regard to the order *Polygalales*, it has not yet been satisfactorily classified: so far no method (morphological, serodiagnostical, or palynological) has presented any plausible interpretation to be universally accepted. In view of a normal diplostemony, it is to be assumed that this is a case of some ancient lateral line, rather celastroid than geraniarutoid, even if the pollen recalls, to some extent, conditions seen in the family *Malpighiaceae*.

Another much contested problem is the relation of the families *Alangiaceae* and *Nyssaceae* which by some botanists are linked up with umbelliferous types or placed rather near to the myrtoid types (recently also by F. A. Novák because of some more important morphological reasons). Erdtmann's studies are more in favour of the first opinion: there are too evident analogies between the pollen-grains of the families *Nyssaceae* and *Cornaceae* on one side and those of the families *Nyssaceae* and *Alangiaceae* on the other. The pollen of the family *Cornaceae* very closely approaches that of the family *Araliaceae*, which again is related to that of the family *Umbelliferae*. On the other hand, there are no such relations to any group of the trend *Guttifero-myrtineae*.

The relative antiquity of the orders belonging to this whole trend (except of course, the relatively derived family *Umbelliferae*) is revealed by some archaic, sporadically preserved characteristics: here and there they still show sieve-tubes of the first Hemenway stage, although they have mostly reached the second stage (the *Umbelliferae* even the third), their vessels are still provided with scalariform perforations, and their wood has no libriform fibres (only tracheides). This agrees with the antiquity of their fossil record.

As decidedly amentiferous derivatives (on grounds stated in the section dealing with amentiferous derivatives) the orders *Garryales*, *Julianales* and *Leitneriales* are assigned to this trend; the first order is to be

linked with the evolutionary umbellifloroid line, all the others, with the celastro-sapindoid line.

The orders *Ligustrales* (or *Oleales*), *Loganiales* (or the narrower orders *Loganiales*, *Apocynales* and *Centianales*) and *Rubiales* are to be regarded as sympetalous derivatives of this trend. This agrees with the current views as to the various morphological and even biochemical analogies. Also Erdtmann's recent palynological discoveries are upon the whole in favour of these relations. In certain respects their pollen resembles that of the representatives of the order *Celastrales* (particularly in the family *Oleaceae* from the order *Ligustrales*) as well as that of the families *Umbelliferae* and *Cornaceae* (especially in the families *Caprifoliaceae* and *Rubiaceae* from the order *Rubiales*). The pollen of the order *Loganiales* is mostly (especially in the family *Loganiaceae*) of a too multifarious nature (eurypalynous types) so that it cannot be relied upon with certainty; only some relations to the family *Rubiaceae* can be ascertained here. Palaeontologically all these plants are of considerable antiquity, because impressions, well comparable with many of them, date from as early as the middle phases of the Cretaceous (Cenomanian). In spite of this many of them reached considerably derived stages even in the anatomical structure (bicol-lateral bundles, intraxylary phloem, latex-tubes). According to the morphological nature and the type of the pollen-grains two lines can be distinguished: the one (orders *Ligustrales* and *Loganiales*) is more narrowly linked with the more original line *Celastrales-Sapindales*, the other (*Rubiales*) with the umbellifloroid line. Besides these three sympetalous orders, also the order *Compositales* (or *Asterales*), which has already been sufficiently discussed with reference to the evolutionary trend *Parietaleae*, might be taken here into consideration as a further sympetalous derivative. Erdtmann's palynological discoveries are more in support of these relations than of their affinities with the parietal types. As, however, this group is very progressive and its pollen shows an enormous variety (it is of a strongly eurypalynous nature) it is very difficult to decide whether in this case the pollen morphology is quite reliable. Erdtmann himself admits that in certain features, of course, to a lesser degree, its pollen is similar to that found in the family *Campanulaceae* which is indisputably related to parietal types. It seems therefore that the relation of the *Compositales* to the parietal types is more probable; this is also the opinion of most taxonomers.

4. Notes on two very old sympetalous plant groups of rather problematic relationship.

Evolutionary trend *Sapoto-primulineae* (Fig. 12).

The old sympetalous trend *Sapoto-primulineae*, including the orders *Ebenales*, *Styracales*, *Myrsinales* and *Primulales*, has already been indirectly outlined by J. Velenovský. It is of an ancient origin, because impressions very probably referring to some of its representatives date from as early as the Cenomanian stage of the Cretaceous (of course, herbaceous *Primulales* excepted). They seem to have attained sympetaly very early, because, in other respects, they have preserved very many archaic features,

which only very rarely occur in sympetalous types of a younger origin; for the most part they have superior ovaries, ovules (the family *Sapotaceae* excepted) with a double integument, and seeds containing sufficient endosperm. As regards the floral morphology, they all have many common features (this has already been pointed out by J. Velenovský): tendencies towards various complications in the androecium not dissimilar

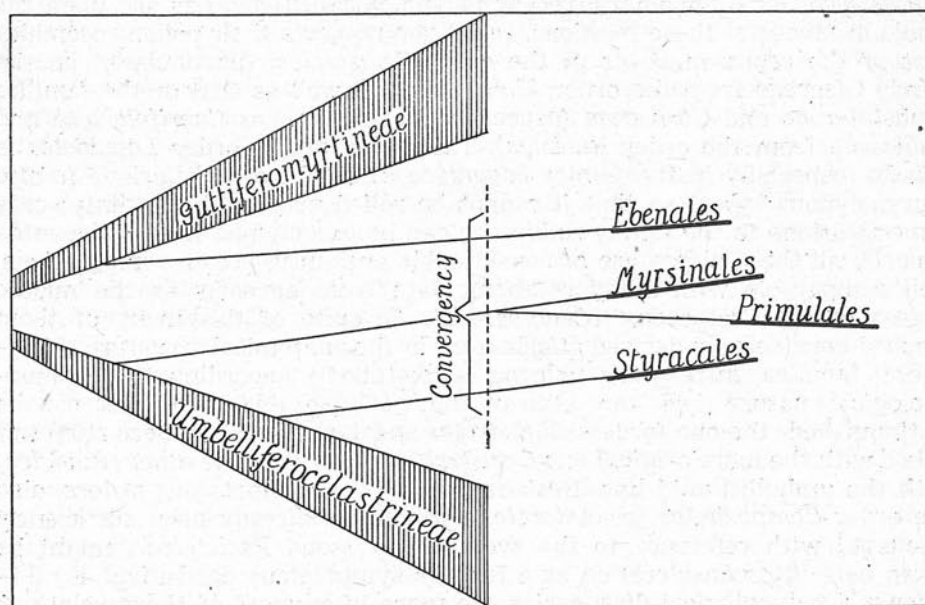


Fig. 12.

Schema vzájemného poměru vývojových linií starého sympetálního okruhu *Sapoto-primulineae*.

Scheme of the mutual relations of the evolutionary lines of the old sympetalous group *Sapoto-primulineae*.

to what is seen in the evolutionary trends *Guttifero-myrtineae* and *Columnifero-tricocceae* (*Ebenales*, *Styracales*) or towards reductions in the androecium to only one epipetalous stamen whorl derived from normal diplostemony (*Myrsinales*, *Primulales*, and the family *Sapotaceae*).

The affinities of this trend have been evaluated in very different ways, the order *Primulales* has even been considered to be related to *Centrospermeae*. Otherwise some relations to the orders *Guttiferales*, *Parietales*, *Rhamnales*, or even directly to the wide line *Ranales-Magnoliales* (our evolutionary trend *Polycarpiceae*) have mostly been suggested. Here, too, Erdtmann's palynological discoveries have, no doubt, contributed much to the solution of these problems. Judging from the nature of pollen grains we may, first of all, assume close relations between the orders *Myrsinales* and *Primulales*. This assumption fully confirms Velenovský's opinion that the *Primulales* represent a herbaceous derivative of the order *Myrsinales*. Their pollen is, however, of a different character from that found

in all centrospermous types as well as the order *Plumbaginales*, from which they are so frequently derived (besides other reasons also for the positive serodiagnosical reactions between the family *Primulaceae* and *Phytolaccaceae*). Palynology is, however, unable to find relations among the orders *Myrsinales*, *Ebenales* and *Styracales*. The order *Ebenales* has a quite isolated position without being more closely related to the trend *Polycarpiceae*, with some members of which it is sometimes directly linked up (Grosgejm). Within the order *Styracales*, Erdtmann discovered certain analogies to the pollen of the members belonging to the umbellifero-ce-lastroid trend (in the family *Styracaceae* to the family *Cornaceae* and *Nyssaceae*, in the family *Symplocaceae* to the family *Icacinaceae*). When, in addition to this, various frequently mentioned morphological phenomena are taken into consideration, it seems to be probable that in this trend there are at least three convergent evolutionary lines. One of them, comprising the order *Ebenales*, may have arisen at some time long ago in the evolutionary trend *Guttifero-myrtineae* (more probably than in the trend *Parietaleae*), the other two (*Myrsinales-Primulales* and *Styracales*) in the umbelliferoce-lastroid trend. The splitting off of the line *Myrsinales-Primulales* might have taken place much earlier than that of the line *Styracales*. It is only in such a way that the palynological relations of the order *Styracales* may have remained more or less recognizable. In other respects various floral changes became reflected in the alterations of pollen-grain sculpturings to such a degree that the true origin of the order is no longer sufficiently clear. Various morphological analogies found especially between the herbaceous order *Primulales* and the order *Plumbaginales* have to be explained by convergences.

Evolutionary trend *Thymelaeo-proteineae* (Fig. 13).

Ancient sympetalous types included into the trend *Thymelaeo-proteineae* belong to the most mysterious groups of the Angiosperms. It was again by Erdtmann's palynological discoveries that new light was cast on their nature and affinities. Following orders (or families in the status of independent orders) make up this trend: *Elaeagnales*, *Thymelaeales*, *Olacales*, *Santalales* (together with the family *Loranthaceae* and its relatives) and *Balanophorales*. It is most interesting that, in spite of a great number of very strongly derived features, many of them (particularly the order *Proteales*) represent the oldest angiospermous types of the Cretaceous flora in general. Many mutual analogies in the floral morphology of the just mentioned orders, which, of course, may have a character of mere convergences, have already been pointed out by J. Velenovský. For various reasons the order *Thymelaeales* is frequently assumed to be most closely related to the order *Myrtales*, and the family *Elaeagnaceae* is placed into its neighbourhood (in this case some investigators suppose relations to the order *Rhamniales*). As to the family *Thymelaeaceae*, the presence of mucilaginous reservoirs quite similar to those of the *Columniferae* is often called attention to. The order *Proteales* has recently been linked up directly with the types of the trend *Polycarpiceae* (Grosgejm, Emberger, F. A. Novák). Finally, as regards the orders *Santalales*, *Olacales* and *Balanophorales*, many investigators (J. Hutchinson, F. A. Novák)

suggest relations to the orders *Celastrales*, others (Grosgejm, Emburger), to the order *Proteales*. It is due to Erdtmann's palynological researches that these mutual relations (or similarities) have been discovered.

The pollen of the order *Thymelaeales* is far from being uniform. In the family *Geisolomataceae* it reveals no special features and shows some

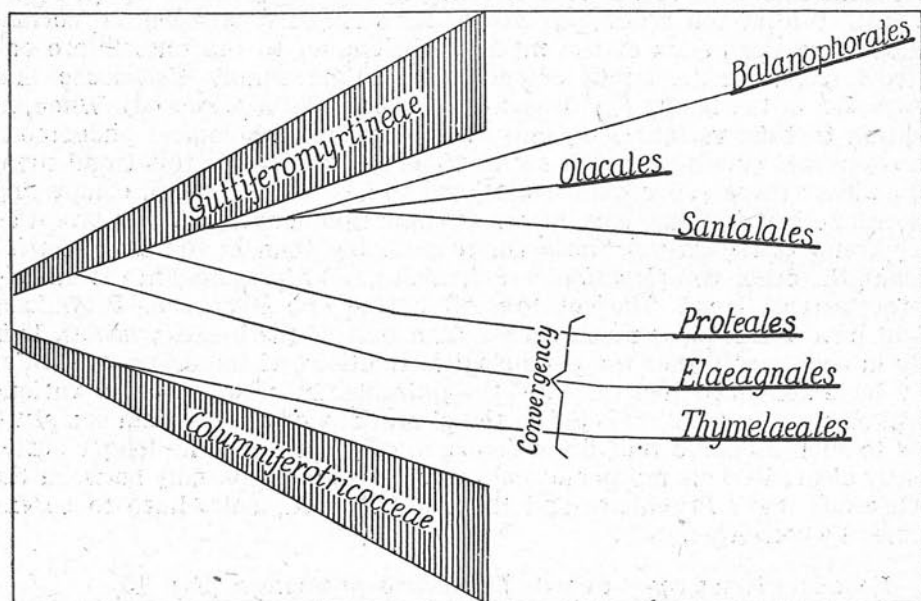


Fig. 13.

Schema vzájemného poměru vývojových linií starého sympetálního okruhu *Thymelaeo-proteineae*.

Scheme of the mutual relations of the evolutionary lines of the old sympetalous group *Thymelaeo-proteineae*.

slight analogies to the pollen of the order *Celastrales*, but decidedly not to that of the other families of the trend under discussion (i. e. the *Thymelaeaceae*, *Elaeagnaceae*, *Penaeaceae*). The pollen of the family *Penaeaceae* has some features in common with that of some families of the order *Lythrales* (*Oliniaceae*, *Lythraceae*). In the family *Elaeagnaceae* there have been found certain similarities to the pollen of the family *Myrtaceae* as well as the *Rhamnaceae*, but no sufficient analogies to the pollen of the families *Proteaceae* or *Thymelaeaceae*. Finally, the pollen of the family *Thymelaeaceae* entirely differs from that of all the mentioned families and strongly reminds of crotonoid pollen-grain types found in the representatives of the family *Euphorbiaceae* (and, therefore, to some extent, also the *Buxaceae*).

According to Erdtmann's researches, the pollen of the family *Proteaceae* indisputably resembles not only that of the families *Olacaceae*, *Santalaceae* and *Balanophoraceae*, but also especially that of the family

Myrtaceae. In the series *Olacales-Santalales-Balanophorales* Erdtmann found many features in common with the pollen of some families of the order *Myrtales*, but no relations at all to the pollen of the representatives of the order *Celastrales*.

Palynologically, in all these cases the relations to the evolutionary trend *Guttifero-myrtineae* have been confirmed, but nothing in common has been found with the trend *Umbellifero-celastrineae*. In the only family *Thymelaeaceae* this method has ascertained relations to the trend *Columnifero-tricocceae*. Desirable may be the revision of affinities in the family *Penaeaceae*, which reveals too distinct relations to the order *Myrtales*, and then in the family *Geisolomataceae*, where certain connections with the order *Celastrales* can be traced. May be that these families do not at all belong to the trend *Thymelaeo-proteineae*.

Unless the peculiarities found in the family *Thymelaeaceae* are to be considered as features (mucilaginous reservoirs, crotonoid pollen) which arose quite independently (i. e. without being due to affinities with the columniferous types)—and this assumption seems to be rather improbable—irrespective of the so far obscure families (*Geisolomataceae* and perhaps also *Penaeaceae*) the brief summary of the mentioned circumstances suggests that the whole trend contains two fundamental evolutionary lines which convergently came very near to each other. The former might embrace the families *Proteaceae*, *Elaeagnaceae* (and perhaps also *Penaeaceae*) together with the whole derived series *Olacales-Santalales-Balanophorales*. It seems to have split off at some time in the very ancient past from the evolutionary trend *Guttifero-myrtineae*. The latter would include only the family *Thymelaeaceae*; its origin is to be looked for in the evolutionary trend *Columnifero-tricocceae*. This assumption is not in contradiction to our palaeontological knowledge, as the remains of myrtaceous types (e. g. *Eucalyptus*) as well as of the representatives of the family *Proteaceae* are known to us from as early a period as the mid-Cretaceous, when Angiosperms actually began to appear on a larger scale.

The whole parallelism in the development of various fundamental members of the whole evolutionary trend *Thymelaeo-proteineae* has also been pointed out by J. Velenovský (particularly that between the families *Thymelaeaceae* and *Proteaceae*). As a matter of fact, the former of the mentioned evolutionary lines represents a group of ultimate members of the evolutionary branches that took entirely different developmental courses: the order *Elaeagnales* (the family *Elaeagnaceae* and, beside it, perhaps also the family *Penaeaceae*) in harmony with normal mesophytic life conditions, the order *Proteales* (the family *Proteaceae*) rather with a tendency towards adaptation to xerothermous conditions, and finally the series *Olacales-Santalales-Balanophorales* with a tendency towards a parasitic life. The flowers have all preserved superior ovaries, only in the parasitic series (*Santalales-Balanophorales*) the ovaries were becoming inferior; this process was accompanied by strong reductions resulting in the loss of integuments (*Olacales* have only one or two integuments or occasionally none at all, integuments are altogether missing in the orders *Santalales* and *Balanophorales*; in some cases even the whole carpels together with the ovules entirely reduced to tissues where one to three

embryo sacs are found embedded). Quite inverse was the case of endosperm: it is well developed in types subjected to strong reductions in other respects, whereas in the others (*Thymelaeales*, *Elaeagnales*) it is weakly developed or even missing entirely (*Proteales*). The other floral parts suffered a particular kind of reductions: only one whorl has been left in the androecium, petals aborted, sepals assume a petal-like appearance, all this led to a seemingly epipetalous position of the stamens. In addition to this, the order *Proteales* reached even a substantial floral zygomorphy and a strong condensation of flowers into head-like inflorescences. Finally, an extreme reduction of the vegetative body can be found in the parasitic series *Olacales-Santalales-Balanophorales*. Provided that the nature of the pollen and the presence of the mucilaginous reservoirs really reveal its true nature, the other evolutionary line, i. e. the order *Thymelaeales* (only the family *Thymelaeaceae*), which is parallel with, and convergent to, the first line (especially to the order *Elaeagnales*), must have diverged from the trend *Columnifero-tricocceae* on very primitive stages, because the nature of the ovaries differs to a certain degree from that found in the orders *Tiliales*, *Malvales* as well as *Euphorbiales*. It is evident that they represent a third branch of the columniferous line, much more archaic than are the *Euphorbiales*.

D. Monocotyledonous Evolutionary Trends (see Fig. 7 and 14).

The fourth section of this paper deals with many phenomena showing clearly that Monocotyledons, as a matter of fact, represent a type derived under the influence of various special life conditions from a more original dicotyledonous type (geophily, hygro- till hydrophily, etc.). Today, hardly any taxonomer would doubt that the source of their origin was our trend *Polycarpiceae*. It is in this trend that we come across most dispositions to the formation of characteristics which did not reach their full development until in the Monocotyledons: ataktostely (in the families *Ranunculaceae*, *Berberidaceae*, *Nymphaeaceae*, there are also cases of it in the families *Papaveraceae*, *Casuarinaceae*, *Chenopodiaceae*, *Amaranthaceae*, *Nyctaginaceae*, and *Phytolaccaceae*, all these being considered in this paper as relatively archaic types), disappearance of one of the two cotyledons, very much derived shape of parallel-veined leaves, polyacunary nodes, collateral arrangement of axillary buds, etc. The monocotyledonous pollen does not show such a variety of forms, as is found in the Dicotyledons; considerably primitive types of a monosulcate nature or derived from this (acolate or asulcate, 1-porous or multiporous grains) predominate. This primitivity and a relative uniformity of the pollen point to a very ancient origin of the whole group as well as to its relative unity and homogeneity (some kind of relative monophyly). In spite of their strongly derived character, many types show their ancient origin by still having sieve-tubes of a more primitive kind (i. e. with considerably oblique cross walls), though in other cases sieve-tubes are already provided with perpendicular cross walls. To such primitive types belong not only some families predominantly consisting of woody plants, i. e. the *Palmae*, *Pandanaceae*, *Dioscoreaceae*, *Smilacaceae*, but also

some genera of the family *Liliaceae* (e. g. the genus *Asparagus*). These types have to be regarded, not as derived types, but as archaic groups giving rise to further development. The relative antiquity of Monocotyledons can, to some extent, be proved palaeontologically. They appear, parallelly with Dicotyledons, as early as the middle phases of the Cretaceous, but always in a subordinate position. It is not until in the Upper Cretaceous and

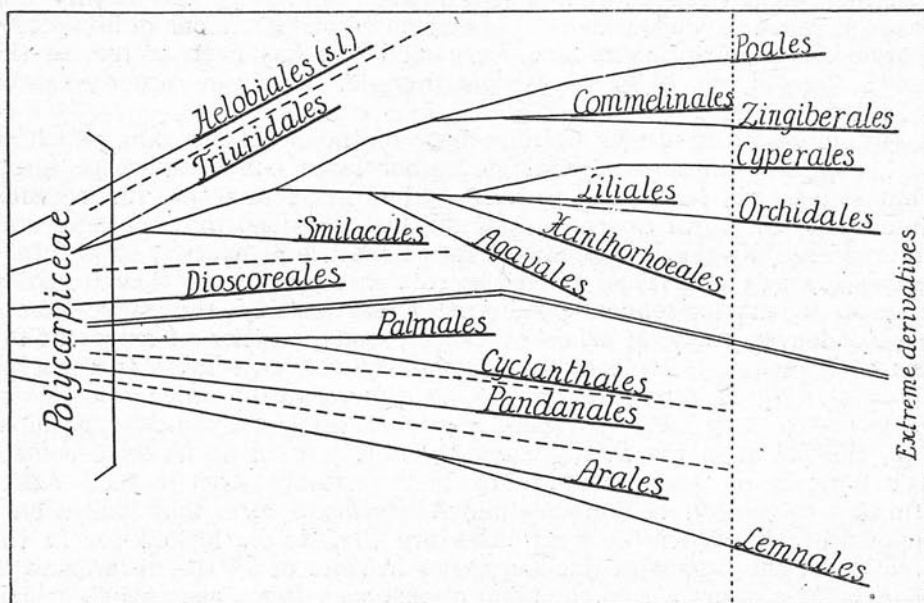


Fig. 14.

Schéma rozpadu části vývojové základní řady *Polycarpiceae* v různé souběžné řady monokotylní.

Scheme of the splitting of a part of the basic evolutionary trend *Polycarpiceae* into the various parallel Monocotyledonous evolutionary lines.

particularly in the Palaeogene that they are becoming more abundant (this is clearly visible in the occurrence of the Palm pollen). This picture is, of course rather imperfect because most herbaceous Monocotyledons, owing to their distribution and nature had no chance of entering as fossils into sedimentary series. On the other hand, the very fact that they become more abundant only as late as the Upper Cretaceous suggests a delay in their development, and, consequently, also their rather late origin as well as their derived character.

Because a great part of Monocotyledons are herbs and woody Monocotyledons reveal a peculiar nature of xylem, many investigators are of the opinion that such woody monocotyledonous types were secondarily derived from the herbaceous ones. This may be true with some particular cases, but on no account with woody plants which disclose more primitive sieve-tubes than do the herbaceous types from which they are thought to arise. The long pedigrees suggested by many botanists for illustrating the

development of the Monocotyledons seem to be as improbable as are those devised to show the evolution of Dicotyledons, and especially those that start from the order *Helobiae* and lead, through the *Liliiflorae* to *Palms* and *Pandanaceae*. It is just the last-named plants that have preserved oblique transverse walls in their sieve-tubes. Here, too, it is very probable that the Monocotyledons represent a set of some parallel series, mutually much more closely related than are the different dicotyledonous evolutionary trends, because they all seem to have originated only from one quite specific dicotyledonous evolutionary line, very likely, as has been stated, of the trend *Polycarpiceae*. In most respects this view has been recently shared by M. Deyl (1954).

In spite of a relatively uniform base of the floral diagram, which so much suggests the idea of a single rather large and complex pedigree, about at least six (according to M. Deyl as many as eight) fundamental evolutionary lines can easily be distinguished, provided that characteristic features are duly taken into consideration (nature of ovaries, special tendencies towards reductions as well as condensations of the flowers, character of pollen, anatomical peculiarities [particularly the sieve-tubes], shape of leaves, mode of origin of axillary buds, position of leaves at the base of branchlets). Some of them appear to converge more to the type represented by the family *Ranunculaceae*, others, to the order *Piperales* or *Aristolochiales*. In the first case there seem to be mere convergences, because, e. g., the pollen in the family *Ranunculaceae* is of a decidedly 3-colpate basic type; in the latter case there may probably exist actual, closer affinities, as the orders *Piperales* and *Aristolochiales* form their pollen on a monosulcate base. The real affinities are then to be looked for in the direction of the proper magnolioid series in spite of all the differences in the general appearance (such monocotyledonous types represent perhaps derived descendants of some types of a mostly herbaceous character, no more existing today and standing between the series of aquatic derivatives *Nymphaeaceae*, as well as *Cabombaceae* and the series of the proper woody *Magnoliales*). The six evolutionary trends included here are the following: *Spathifloreae*, *Pandanoideae*, *Palmo-synanthaeae*, *Lilio-agavoideae*, *Dioscoreoideae*, and *Helobiae*.

The trend *Lilio-agavoideae* represents today a central monocotyledonous type which is most widespread and most diversified so far as its special further derivatives are concerned. According to the author's classification they embrace the orders *Liliales*, *Cyperales*, *Microspermales* (*Orchidales*), Hutchinson's order *Agavales*, the genus *Xanthorrhoea* in the status of the order *Xanthorrhoeales* (i. e., to some extent, in the sense of Deyl's monocotyledonous "xeranthemous" type), the family *Smilacaceae* in the status of the order *Smilacales*, *Glumiflorales* (*Poales*), *Triuridales*, *Commelinales* and *Zingiberales*. It is in this trend that almost all taxonomers look for—and they are to a great extent right in doing so—the common stock of the four following extreme courses of evolution: (a) connected with the order *Commelinales* is the order *Zingiberales*, an extremely entomophilous derivative with a pronounced tendency towards zygomorphy as well as irregular floral structure, and the order *Glumiflorales* (*Poales*), a derivative which shows a tendency towards extreme

anemophily and reduction of flowers of gramineous nature; (b) similarly linked with the order *Liliales* are the entomophilous zygomorphic *Microspermales* (*Orchidales*) and the gramineous anemophilous *Cyperales* with reduced flowers. — Besides these extreme derivatives tending towards a special floral arrangement, two more lines with a tendency towards becoming woody (which is evidently a secondary phenomenon, derived from herbaceous types) can be clearly distinguished: (c) on one hand Hutchinson's order *Agavales*, the origin of which is assumed by many authors to be biphyletic (arising partly from the affinities of the family *Liliaceae* and partly from that of the family *Amaryllidaceae*; Hutchinson's view has been recently shared and supported by M. Deyl), (d) on the other hand the relationship of the genus *Xanthorrhoea* in the status of the order *Xanthorrhoeales*, representing to a great extent what M. Deyl calls "xeranthemous" type. Finally, besides all these types that for the most part still retain their full vigour and can be regarded as derived and ecologically specialized evolutionary branches of the two fundamental orders *Liliales* and *Commelinales*, the trend *Lilio-agavoideae* includes two more types of an evidently relict character, which also owing to morphological reasons cannot be separated from it, i. e. the *Smilacales* and *Triuridales*. Some light has now to be thrown on their nature.

Because of its apocarpous gynoeceum the order *Triuridales* (with the only saprophytic family *Triuridaceae*) is often placed into the trend *Helobiaeae*. It differs, however, from it in having a well-developed endosperm. Palynology does not reveal much in this case; according to Erdtmann, the pollen is of a very much reduced nature (rounded and nonaperturate), which is evidently in connection with its saprophytic life. Some explanation as to its relations is afforded by its comparison with the genus *Petrosavia* (also a saprophyte), assigned, perhaps with full right to the order *Liliales*. Its ovaries are only partially fused at the base, and show thus clearly a transitory stage. It is apparently due to the saprophytism that the original archaic state has been preserved here, just as in other cases (see, e. g., pteridophytic relicts *Psilotum* and *Tmesipteris*). Its relation to the order *Liliales* is, therefore, very close.

Also the order *Smilacales* (with the only genus *Smilax*) is, no doubt, in many respects very nearly related to the order *Liliales*, especially the family *Liliaceae*. It differs, however, most remarkably from it not only in the general arrangement of leaves ("dicotyledonous" type), but also in the orientation of the first scale-shaped leaflets on the branches (see J. Velenovský) and in a different orientation of the embryo in the seed (its position is not central, in the axis of the seed, but excentric in the endosperm). From the palaeontological point of view it is a very old type, very well developed as early as the Late Cretaceous. It seems to have separated from the main evolutionary lilioagavoid trend very early (like the *Triuridales*) and to have retained, in some respects, more archaic characteristics because of a considerable specialization for greatly xerothermous conditions; on the contrary, the development of other members of this trend was for the most part influenced by strong tendencies towards geophily.

From all this it follows that the *Triuridales*, as well as the *Smilacales*,

represent, within the lilioagavoid trend, two interesting blind lateral lines which, due to special life conditions, became arrested on certain stages, less progressive, when compared with the development attained by most representatives of the whole trend.

The evolutionary trend *Dioscoreoideae*, including the only order *Dioscoreales*, most frequently assigned to the order *Liliales* in the status of a mere family, recalls by its various features (shape and venation of leaves, serial arrangement of the buds at leaf axils, transversal position of the first leaves on branches, collateral vascular bundles still found at least in young branchlets) the dicotyledons far more than the Monocotyledons. Clear analogies (both in flowers and fruits) with the order *Aristolochiales* have been duly pointed out already by J. Velenovský. This trend has therefore nothing in common with the lilioagavoid evolutionary trend itself and obviously represents an ancient relict, which, of all the Monocotyledons, may stand nearest to their dicotyledonous ancestors.

The evolutionary trend *Helobieae*.—As all taxonomic compendia so far published show, the evolutionary trend *Helobieae* represents a series of rather isolated types formerly included into the order *Helobiales* (or else *Alismales*). The development of all of them took place under the influence of a pronounced tendency towards hydrophyly, and, in a sense, convergently to many phenomena found in the dicotyledonous *Ranunculales*, *Nymphaeales*, as well as other orders of the trend *Polycarpiceae*. It is just owing to such extreme and apparently very early adaptations to special life conditions that, of all the monocotyledonous groups they advanced least. More or less they all preserved their apocarpous gynoecia. A rather substantial progressivity, of course, also of a reductional character, is revealed here only by the loss of endosperm. In other respects, their development tended towards various slighter reductions affecting floral parts, pollen-grains (mostly simplified, nonaperturate pollen-grains) as well as anatomy of axes—all this obviously being connected with their aquatic environment. Many taxonomers attach here a great importance to the so-called squamulae intravaginales which they consider to be an outstanding characteristic showing a considerable uniformity of this group (e. g. M. Deyl), although J. Velenovský points to the presence of such scales also in other aquatic Monocotyledons (e. g. the genus *Acorus*). Another outstanding feature of this trend is seen by many botanists in the formation of hibernative buds (the so-called hibernaculae). In other respects an amazing variety in forms lead the more recent systematists to distinguish here a greater number of orders. Very often this trend is regarded as a center of development and all the other Monocotyledons are derived from it. This assumption is, however, quite erroneous, because this whole group represents, as a matter of fact, only a blind and extremely specialized branch. On the other hand, it must be admitted that, of all the Monocotyledons, it has preserved the most archaic type of flowers, which give us an idea of what the flowers of the ancestors of the present-day Monocotyledons might have looked like.

The evolutionary trend *Spathifloreae*.—As regards the appearance and floral reductions, the evolutionary trend *Spathifloreae*,

including the only predominantly herbaceous order *Arales*, is the one of all the monocotyledonous trends which most converges to the type *Piperales*. This phenomenon was by many taxonomers considered as proof of actual affinities. The *Spathifloreae* show a marked tendency towards strong floral reductions accompanied by a condensation of flowers into dense spadix-like inflorescences protected by characteristic spathes. This reductional tendency is especially evident in hydrophilous types where even the number of flower on the spadix occasionally strongly decreases, e. g. in the genus *Pistia*, to only two (one male with two stamens and one female with a small one-carpel ovary). By the majority of taxonomers also the typical aquatic derivative, the family *Lemnaceae*, is brought into connection with these strongly reduced aquatic types. Detailed and most ingenious researches concerning these affinities were made by J. Velenovský from the morphological point of view. Palynologically Erdtmann has discovered that the pollen-grains of this family stand nearest to those of many representatives of the family *Araceae* and that only some of their features slightly recall the pollen of the family *Najadaceae*. He also found a somewhat similar pollen in some genera of the family *Zonnicelliaceae* (particularly in the genus *Zannichellia*). The pollen of the group *Helobieae* is, of course, strongly reduced and nonaperturate, whereas in the family *Lemnaceae* it is monoaperturate. In spite of all this some botanists also (M. Deyl) have raised serious objections to the derivation of the family *Lemnaceae* from the family *Araceae* and considered its relations to the trend *Helobieae* as more probable. Their opinion is based mainly on the following phenomena: some points of resemblance in the arrangement of the stigmas, certain analogy between the hibernaculae of some representatives of the group *Helobieae* and the leaflets resp. segments of the *Lemnaceae*, discovery of squamulae intravaginales found in the genus *Spirodela* and some superficial similarity of its pollen to that of the genus *Zannichellia*. To solve this problem quite objectively is surely very difficult, because various convergences found in these plants so extremely adjusted to aquatic life and so strongly reduced may, after all, appear to be actual affinities. It is surprising that the family *Lemnaceae* has preserved a monoporate pollen type and the seed endosperm, whereas the trend *Helobieae* shows a marked tendency towards a strong reduction of the pollen (all grains are nonaperturate) as well as the loss of the endosperm (missing everywhere). This striking difference is more in favour of the older theory (J. Velenovský) suggesting relations of the *Lemnaceae* to the trend *Spathifloreae*.

The evolutionary trend *Pandanoideae*, embracing besides a great number of herbaceous elements also many woody plants developed rather more distantly from the type *Piperales* than did the trend *Spathifloreae*. Here, too, there is a strong tendency towards the reduction of tiny flowers to mere naked stamens and small ovaries. The antiquity of this line and, consequently, its considerable independence on other monocotyledonous evolutionary trends is confirmed in a most conspicuous way not only anatomically by the presence of still oblique cross walls in the sieve-tubes of some genera, but also by fossil evidence: impressions of plants quite similar to the present-day representatives appear as early as the Creta-

ceous, some even by the close of the Lower Cretaceous. Otherwise they occur rather parallelly with the remains of the Palms.

The evolutionary Palm trend *Palmo-synanthaeae*, including the orders *Palmales* (*Principes* or *Arecales*) and *Cyclanthales* developed most remotely from the type *Piperales* and in the nearest neighbourhood of, and parallelly to, the central main monocotyledonous type, the evolutionary trend *Lilioagavoideae*. That it arose near the trend *Lilio-agavoideae*, is indisputably indicated by a great number of morphological features found in the floral arrangement. The mutual parallelism is chiefly proved by the fact that the Palms as well as some representatives of the lilioagavoid trend display apocarpous, or almost apocarpous, ovaries (the Palm group *Coryphoideae*, the lilioagavoid *Triuridales* and the genus *Petrosavia*) and an archaic type of sieve-tubes (e. g. the lilioagavoid genus *Asparagus* or the order *Smilacales*). The antiquity and independent origin of the Palms is further indicated by the appearance of dichotomous branching (in the genus *Hyphaene*), by the preservation of seed endosperm, and, last but not least, by fossil record: their remains known to us with certainty date from the Turonian stage of the Cretaceous, it is, of course, not until the Senonian stage that they become more abundant. They are exclusively woody plants. — The other order *Cyclanthales* embraces besides woody types also herbaceous elements. In view of the morphology of their flowers they are often with full right considered to be a type affected by strong floral reductions and by a considerable condensation of flowers into dense inflorescences, a type which represents a collateral derived branch of Palms tending to produce herbaceous forms. It is no doubt, an evolutionary branch, which due to strong convergences considerably approaches the evolutionary trend *Pandanoideae*.

The last three mentioned monocotyledonous evolutionary trends *Spathifloreae*, *Pandanoideae* and *Palmo-synanthaeae* stand doubtlessly nearer to each other than to the other monocotyledonous trends discussed in this paper. The Palms approach most the liliaceous type. But in view of various anatomic features, some morphological conditions and old geologic age it is to be assumed that this relation represents nothing more than the parallelism of these trends. The mutual relation of the three just mentioned trends seems to be as follows: the bulk of the trend *Pandanoideae* has reached about the same stage of development as have the more advanced representatives of the trend *Palmo-synanthaeae*; it also contains a much greater number of herbaceous types. In this light the trend *Spathifloreae* again reminds of the more advanced stages attained by the trend *Pandanoideae*. Here the herbaceous element is already predominating and the development went even so far as to form altogether hydrophilous and extremely reduced derivatives. These relations doubtlessly revealing a successive development from the normal, terrestrial and woody types to different herbaceous, geophilous, hygrophilous and even aquatic derivatives are rather suggestive of considering these three evolutionary trends as mere members of a single gradually proceeding evolutionary line. Nevertheless, in spite of this so striking a phenomenon (which is often evaluated in the same way in the majority of diagrams showing the development of Monocotyledons), it is to be assumed that three considerably

independent and parallel evolutionary trends are concerned here. This assumption is particularly supported by some mentioned primitive characteristics shown by the woody plants belonging to these trends. If this were not the case, the supposition that such characteristics found in successively more derived lines should give way to more progressive feature would be more plausible. Another reason in favour of this supposition can be seen in their occurrence during the geological past: it is hardly imaginable that such a long genealogic process should have taken place within so short a period to be allotted to the whole development of these trends as well as to their separation from a common dicotyledonous and polycarpous stock.

VII. Rough Outline of the System of Angiosperms divided into the single Parallel Evolutionary Trends or Lines.

I. *Dicotyledones*.

A. Evolutionary trends with flowers supposed to be of heterogenous character.

a) Evol. trends arrested on the first evolutionary stage.

1. *Trochodendrineae*

Orders: *Trochodendrales* (only the families *Trochodendraceae* and *Tetracentraceae*).

b) Evol. trends arrested on the second evolutionary stage.

2. *Eucommio-cercidiphyllineae*

Orders: *Eucommiales*, *Cercidiphyllales*.

3. *Amentiferineae*

Orders:

evolutionary line *Fagoideae*: *Balanopsidales*, *Fagales*,

evol. line *Myricoideae*: *Myricales*,

evol. line *Verticilloideae*: *Casuarinales*.

4. *Urtico-platanineae*

Orders:

evol. line *Rhoipteleoideae*: *Rhoipteleales*,

evol. line *Platanoideae*: *Platanales*,

evol. line *Urticoideae*: *Urticales*.

c) Evol. trends which attained the third evol. stage.

5. *Centrospermineae*

Orders:

basic. evol. line *Polygonoideae*: *Polygonales*,

basic evol. line *Chenopodio-caryophylloideae*:

the lateral proper chenopodio-caryophylloid line: *Chenopodiales* (incl. the sympetalous derivative *Amarantaceae*),
Caryophyllales,

sympet. deriv.: *Plumbaginales*,

the lateral phytolaccoid line: *Phytolaccales*,

sympet. deriv.: *Nyctaginales*,

amentif. deriv.: *Batidales*,

succulent deriv.: *Aizoales*,
the lateral cactoid line: *Opuntiales*.

6. *Geranio-rhamnineae*

Orders:

evol. line *Geranio-rutoideae*: *Geraniales* (the *Tropaeolaceae*
and *Balsaminaceae* perhaps excepted) *Malpighiales*, *Ruta-*
les, *Melilales*,

sympet. deriv.: *Ericales* (incl. *Empetraceae*),

evol. line *Buxoideae*: *Buxales*,

evol. line *Rhamnoidae*: *Rhamnales*.

B. Evol. trends with flowers supposed to be of homogenous character.

a) Evol. trends arrested on the first evolutionary stage.

1. *Polycarpiceae*

Orders:

evol. line *Magnolio-annonoideae*: *Winterales*, *Degeneriales*,
Magnoliales, *Annonales*,

sympet. deriv.: *Myristicales*, *Aristolochiales*
(incl. *Rafflesiaceae* and *Hydnoraceae*),

amentif. deriv.: *Piperales*, *Hydrostachyales*,

aquatic deriv.: *Nymphaeales*, *Ceratophyllales*,

evol. line *Callicantho-lauroideae*: *Laurales*, *Callicanthales*,
amentif. deriv.: *Chloranthales*,

evol. line *Schizandro-ranunculoideae*: *Eupteleales*,
Schizandrals, *Paeoniales*, *Ranunculales*,

aquatic deriv.: *Nelumbiales*,

evol. line *Berberido-menispermoideae*: *Berberidales*,
Menispermals.

b) Evol. trends arrested on the second evolutionary stage.

2. *Dilleniineae*

Orders: *Dilleniales*, *Pittosporales*, *Coriariales*.

3. *Canellineae*

Orders: *Canellales*.

4. *Hamamelidineae*

Orders: *Hamamelidales* (incl. *Balsamifluae* [i. e. *Liquidambar*];
excl. *Platanaceae*),

amentif. deriv.: *Myrothamnales* (i. e. *Myrothamnaceae*).

5. *Rhoeadineae*

Orders: *Rhoeadales* (sensu str. [Hutchinson]),

insectivorous deriv.: *Sarraceniales* (only *Sarraceniaceae*).

c) Evol. trends which attained the third evolutionary stage.

6. *Cruciferineae*

Orders: *Capparidales* (incl. *Bretschneideriaceae*), *Cruciferales*.

7. *Parietaleae*

Orders:

the dillenioid evol. line: *Bixales* (excl. *Canellaceae*),

Tamaricales, *Passiflorales*, *Violales*,

amentif. deriv.: *Stachyurales* (i. e. *Stachyuraceae*), *La-*
cisternales, *Salicales*.

sympet. deriv.: *Cucurbitales*, *Campanulales*, *Asterales* (incl. *Calyceraceae*).

the rhoeadoid evol. line: *Resedales*, *Loasales*.

8. *Saxifrago-rosineae*

Orders:

evol. line *Rosoideae*: *Cunoniales Saxifragales* (incl. the succulent deriv. *Crassulaceae* and the insectivorous deriv. *Cephalotaceae*), *Rosales*,

insectivorous deriv.: *Nepenthales* (i. e. *Nepenthaceae* and *Droseraceae*),

aquatic deriv.: *Podostemonales*,

sympet. deriv. "Tubiflorae": *Plantaginales*, *Polemoniales*, *Borranginales* (incl. the aquatic deriv. *Callitrichaceae*), *Solanales*, *Convolvulales* (with the parasitic deriv. *Cuscutaceae*), *Personales* (with the aquatic deriv. *Lentibulariaceae* and the parasitic deriv. *Orobanchaceae*), *Lamiales*,

evol. line *Papilionoideae*: *Leguminosales*.

9. *Columnifero-tricocceae*

Orders: *Tiliales*, *Malvales*, *Euphorbiales*.

10. *Guttifero-myrtineae*

Orders: *Theales*, *Guttiferales*, *Myrtales*, *Lythrales* (incl. *Punicaceae*),

aquatic deriv.: *Hydrocaryales* (*Trappaceae*), *Haloragales* (*Haloragaceae* and *Gunneraceae*), *Hippuridales* (*Hippuridaceae*),

parasitic deriv.: *Cynomoriales*.

11. *Umbelliferocelastrineae*

Orders:

evol. line *Umbellifloroideae*: *Umbelliflorales* (incl. *Nyssaceae* and *Alangiaceae*),

amentif. deriv.: *Garryales*.

evol. line *Celastro-sapindoideae*: *Celastrales*, *Pandales*, *Sapindales* (incl. *Didiereaceae*), *Polygalales*,

amentif. deriv.: *Juglandales*, *Julianales*, *Leitneriales*,

sympet. deriv.: *Ligustrales*, *Loganiales* (i. e. *Loganiales* s. str., *Apocynales* and *Gentianales*), *Rubiales*.

d) Old sympetalous derivatives of rather problematic relationship

1. *Sapoto-primulineae*

Orders:

convergent evol. lines exhibiting relations to the evol. trend *Guttifero-myrtineae*: *Ebenales*,

convergent evol. lines exhibiting relations to the evol. trend *Umbellifero-celastrineae*: *Styracales*, *Myrsinales*, *Primulales*.

2. *Thymelaeo-proteineae*

Orders:

convergent evol. lines exhibiting relations to the evol. trend

Columnifero-tricocceae: *Thymelaeales* (only the fam. *Thymelaeaceae*),
convergent evol. lines exhibiting relations to the evol. trend
Guttifero-myrtineae: *Elaeagnales*, *Proteales*, *Olacales*,
parasitic deriv.: *Santalales*, *Balanophorales*.

II. *Monocotyledones*.

1. *Helobieae*

Orders: *Helobiales* (event. a larger number of narrower defined orders).

2. *Lilioagavoideae*

Orders: *Triuridales*, *Liliales*, *Cyperales*, *Orchidales*, *Poales* (or *Glumiflorales*), *Zingiberales*, *Agavales*, *Xanthorrhoeales*, *Smilacales*.

3. *Palmo-synantheae*

Orders: *Palmales* (or *Arecales*), *Cyclanthales*.

4. *Pandanoideae*

Orders: *Pandanales*.

5. *Spathifloreae*

Orders: *Arales*,

aquatic deriv. (not yet safely proved): *Lemnales*.

6. *Dioscoreoideae*

Orders: *Dioscoreales*.

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