

PARALLELISM AND ITS SIGNIFICANCE FOR THE SYSTEMATICS OF FOSSIL PLANTS

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ABSTRACT

With growing studies of fossil plants in fine detail as well as with establishing connections between fertile and sterile plant remains, one now and again comes across parallelism phenomena, which may be manifested in the appearance of similar morphological types and similar series of variations in different systematical groups. Examples of such series among pteridosperms, cycadophytes and other fossil plants are presented. The causes of the parallelism are often searched in adaptation to similar environmental conditions. Remarkable recurrence of quite a number of series of morphological types in different groups, inhabiting various environments in various times suggests, however, that at least partly some inherent qualities of the plant organisation are at the bottom of the parallelism. Since parallelism is a widespread evolutionary phenomenon one has to take it into consideration during a taxonomical treatment of fossil plants. Some corresponding methods of fossil plant taxonomy are suggested.

The main principles of the systematics of fossil plants were worked out during the first third of XIXth century, i.e. immediately after palaeobotanists recognized that a number of plant fossils belong to extinct groups. The taxonomic treatment of these plants, which were hardly comparable with living genera, was of two kinds. If fertile and sterile parts were known in organic connection, their taxonomic treatment was like that in neobotany. For plant remains which are too peculiar or, on the other hand, show no salient characters (to be placed into existent classification of living plants) a code of the systematical features of once and for all established value has been accepted. The code for plant megafossils was completed by the end of XIXth century, that for miospores by the sixties of this century. This code was a basis for delimitation of genera like *Sphenopteris*, *Pecopteris*, *Phyllothea*, *Equisettites*, *Lepidodendron*, *Samaropsis*, *Leiotriletes*, *Verrucosisporites*, etc.

This universally adopted palaeobotanical systematics arose from the investigation of the Palaeozoic-Mesozoic plants mainly of Western Europe and for a long time it did not show defects too significant for its revision. Of course, with continuing investigations, especially of floras of other regions, the systematics was completed, but the very principles of genera establishment remained fundamentally unchanged.

In recent years, however, with growing detailed investigations of plant remains with modern methods, in the delineations of the genera, including classical ones, serious shortcomings were recognized. Now and again palaeobotanists come across cases, when similar looking plants have proved to be unrelated and, on the contrary, leaves and other parts of plant body, having a few features in common in general appearance, have proved to belong to a single family or even genus. I have no doubt, that to some extent palaeobotanists always bore in mind the formality of the taxa adopted by them. But in stratigraphical, phytogeographical and evolutionary studies they often treated these taxa as principally corresponding to natural ones, though somewhat distinct from them in their bulk. Only a

rather limited number of genera like *Sphenopteris*, *Samaropsis* and others are commonly considered notoriously formal.

The history of the studies of Angara and Gondwana Upper Palaeozoic plants shows a good deal of examples of consequent misinterpretations. It was believed, that many plants and floras themselves are closely related. In reality their similarity is mostly a result of the parallelism (MEYEN, 1967-1969). Similar situation has been observed in the comparison between the Upper Palaeozoic plants of Cathaysia and S.W. United States (ASAMA, 1966; MAMAY, 1968), whose similarity is also mainly superficial.

Such situations are well known to every palaeobotanist. The cases, when palaeobotanists referred unrelated plants to the same natural genus on the basis of external similarity alone, or taxonomically separated closely related plants, are too familiar to everybody to be further discussed. It seems evident that it is high time to see in these multiple examples not any annoying exception of a good rule, but a new rule, denying or at least completing the old habitual ones. An attempt to derive some lessons from previously made errors is the subject of the paper.

At the first sight there is only one such lesson, i.e. to study material more carefully to prevent further errors. But this observation is only partly justified. Firstly, a material may be unsatisfactorily preserved so as to respond to relevant techniques. Secondly, many errors arise due to misinterpretations rather than the scarcity of observations.

EXAMPLES OF PARALLELISM IN FOSSIL PLANTS

The external resemblance, unsupported by the natural relationship, may be divided into two types of situations.

First type (A), which is more often recorded, shows the similarity of individual organs of different plants or individual plants of different affinities. Another type (B) is more complicated and covers the similarity of not individual morphological types but a whole series of them clumped into two or more systematical groups. Type B corresponds to Vavilov's (1922) law of homologous series in hereditary variation. The delimitation of both types is quite conditional and type A is often a special (partial) case of type B. Let us see now the corresponding examples.

Type A: This type can comprise independently arisen similarity of both sterile and fertile parts. A classical example of the repetition of the gross morphology in a single organ (leaf) is seen in the form genus *Taeniopteris*, comprising nearly identical leaves, whose parental plants might belong to the ferns, pteridosperms, cycads, bennettites and pentoxyles. More complete similarity, covering nearly the whole soma, is shown by the Angara and Gondwana *Phyllothecca*-like plants, belonging to different families (Tschernoviaceae and Gondwanotachyaceae respectively) but having strikingly similar vegetative shoots (MEYEN, 1969a, 1971). It is true that the anatomical structure of Angara phyllothecas is unknown as yet, and hence one cannot judge on the similarity of fine details. The likeness of the Lower Gondwana *Buriadia* with the northern Upper Palaeozoic—Lower Mesozoic conifers can be seen in the structure of wood, epidermis and in the gross morphology, the reproductive parts being quite different. An example of the similarity of the latter is seen in seed scale of the conifer genus *Ullmannia* and seed scales of Angara genera *Cardiolepis* (leaves of this plant belong to the genus *Phylladoderma*) and *Slivkovia*, which, judging from their leaf structure, are of quite different affinities. Such cases are very characteristic for the higher plants, and further examples would be superfluous.

Type B: Unlike similarity of individual organs or entire plants, the reiteration of the series of variation in different groups received much less attention. Therefore, the corres-

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ponding examples will be presented herein in a fuller way. In the series that follow (Text-fig. 1), the genera are not equivalent to each other, and sometimes seem to represent only more or less isolated groups of species within a more comprehensive genus. On the other hand, some genera in reality may include several closely related natural genera. During the construction of the series on the basis of morphological and anatomical features, the geographical and stratigraphical distribution has also been taken into consideration.

SERIES	GENERALIZED MORPHOLOGICAL TYPES							
GLOSSOPTERIDS SERIES								
NILSSONIOPTERIS SERIES								
CTENIS SERIES								
PELTASPERMACEOUS SERIES								
PARAGONDWANIDIUM SERIES								
CORYSTOSPERMACEOUS SERIES								
PACHYPTERIS SERIES								
ARCHAEOPTERIS SERIES								

Text-Fig. 1.—The distribution of some morphological types of the foliage leaves within series; leaf morphology is shown schematically. 1. *Rubidgea* and pre-Glossopterids; 2. *Rhabdotaenia*; 3. *Glossopteris*; 4. *Pteronilssonina*; 5. *Nilssoniopteris*; 6. *Pterophyllum*; 7. *Dictyozamites*; 8. *Otozamites*; 9. *Doratophyllum* and *Macrotaeniopteris*; 10. *Anthrophyopsis*; 11. *Pseudoclenis*; 12. *Ctenis*; 13. *Amdrupia* and *Zamiopsis* (?); 14. *Tatarina*; 15. *Scytophyllum*; 16. *Lepidopteris*; 17. *Angaridium mongolicum*; 18. *Paragondwanidium sibiricum*; 19. *Paragondwanidium kumpanii*; 20. *Dicroidium hughesii*; 21. *Dicroidium odontopteroides*, *D. feistmantlii*, *Hoegia papillata*; 22, 23. *Pachypteris*; 24. *Eddya*; 25. *Archaeopteris*.

Fam. Peltaspermaeae. This family comprises the Permian *Tatarina* (MEYEN, 1969) and Triassic *Scytophyllum* (DOBRUSKINA, 1969) and *Lepidopteris* (also known in the Permian). HARRIS (1932) drew together *Lepidopteris* and *Ptilozamites*, which was sometimes erroneously referred to cycads. The first three genera show a large number of epidermal types. Some *Scytophyllum* with characteristic once-pinnate fronds are more similar in their epidermal structure to certain *Lepidopteris* than to the other members of *Scytophyllum* (DOBRUSKINA, 1969). The same can be said about the relation of epidermal types of *Tatarina* and *Scytophyllum*. There is a morphological transition between the genera *Scytophyllum* and *Lepidopteris*. Transitional forms between once-pinnate *Scytophyllum* and simple leaved *Tatarina* are not known, though among *Pursongia** (this genus comprises *Tatarina*-like leaves without

*The species *P. tungusana* Neub. and *P. mongolica* Neub. do not belong to the genus and on the formal grounds can be ascribed to *Glossopteris* (Zimina, 1967; Meyen, 1969).

cuticle preserved) there are leaves with dissected margin, e.g. *P. serrata* (Srebr.) S. Meyen.

The usual delimitation of the genera *Scytophyllum*, *Lepidopteris* and *Tatarina* is based on the gross morphology of the leaf. If the delimitation is correct, one can observe parallel series of variation in the cuticle topography and stomatal structure. If we modify the systematics of the family on the basis of epidermal features, the series will stand in general leaf organization.

In their cuticle structure and partly gross morphology the genera *Comia*, *Compsopteris* and *Callipteris* subgen. *Feonia* of the Upper Permian Angara flora are related to the peltasperms (MEYEN and MIGDISOVA, 1969). The species of these genera can be arranged in a single series. At the beginning of the series once-pinnate *Compsopteris* can be placed. Its secondary (lateral) veins are more or less regularly repeatedly forked and groups of the veins resulted do not show distinct central vein; pinnule margin is entire. In *Comia primitiva* Neub. the groups of secondary veins show an incipient central vein, and intermediate veins occur between the groups; the margin is entire as well. In other *Comia* species the groups of secondary veins become more complicated, the margin correspondingly shows progressive dissection. The intermediate veins become forked (once to several times) and/or more numerous. In *C. dentata* Radcz. every group corresponds to a well developed lobe. The pinnules of *C. dobrolubovae* Tschal. are more similar to *Callipteris* pinnae with basally fused pinnules. In some *Comia* the main rachis shows wide and sometimes lobed wings with venation. The wings can be correlated with fused intermediate pinnules of *Callipteris*. The epidermal types among *Callipteris* subgen. *Feonia* and *Compsopteris* are common.

Thus, one can see here the same trend of frond variation as in typical peltasperms, but there are some differences: (1) this series lacks simple leaves; (2) all veins of the fused pinnules* enter the margin, whereas in *Scytophyllum* lateral veins of such pinnules end at the same place as if the pinnules were free; (3) the pinnules of all the representatives have the distinct midrib and no forms like *Ptilozamites* have been discovered yet ("*Dicroidium*" *adzvaeanum* Zalessky, 1934, undoubtedly belonging to another genus, can be compared with *Ptilozamites* in this feature).

Ctenis series. HARRIS (1932) united the genera *Ctenis*, *Pseudoctenis*, *Quervainea* and *Macrotaeniopteris* from the Lower Mesozoic of Greenland into the *Ctenis* series, based on epidermal features. He suggested that *Anthrophyopsis*, *Amdrupia* and some *Doratophyllum* also may belong to the series, but he refrained from the inclusion of *Anthrophyopsis* and *Ctenis* into a single series due to their different morphology, though in their epidermal features *A. crassinervis* Nath. and *C. fallax* Nath. are nearly indistinguishable.

Above mentioned genera can be variously arranged in a series. One can begin with *Macrotaeniopteris* and *Doratophyllum*. The dissection of such leaves leads us to *Pseudoctenis*, and the adding of anastomoses to *Ctenis*. Reverse fusion of the pinnules of the latter gives *Anthrophyopsis*. The formation of midrib in *Ctenis* pinnules leads to *Quervainea*. The lobing of margin of its pinnules leads to *Amdrupia*. It is of interest that the margin of Jurassic *Anthrophyopsis* from Caucasus is lobed (personal communication of M. P. Doludenko). The transformation of leaf morphology within *Ctenis* series is evidently similar to those in pteridoperms as stated above.

A group of parallel genera with and without anastomoses are known for a long time

*For such fused pinnules, retaining original distribution of veins, a new term "pinnuloid" may be proposed.

from the Upper Palaeozoic Euramerican flora. These are: *Alethopteris*—*Lonchopteris*, *Neuropteris*—*Reticulopteris*, *Paripteris*—*Linopteris*, *Pecopteris*—*Palaeoweichselia*, *Odontopteris*—*Anastomopteris*. The first three pairs of the genera are represented by sufficient number of species to see significant variation in the general organization of the frond. The trend of the variation in both members of every pair repeats itself. To ascertain this, one can take for analysis both specific features and those which are considered to vary within a species. These are pinnule outline, their compact or distant insertion on the rachis, variation in pinnule dissection from the apex of the pinna to its base, the position of the midvein, presence of wings on the rachis, distinct or standard appearance of the basal pinnule of the basicopic row (in particular its transformation into reduced pinna), etc. Similar trends in variation are revealed by comparison of the members of different pairs. The genera *Lonchopteris* and *Linopteris* can be divided into analogous groups on the basis of a degree of the reticulate venation development. In some species of both genera the anastomoses completely obscure the general direction of the lateral veins, whereas in other species the latter are clearly traced and anastomoses occur mostly in peripheral part of the lamina. Within these groups similar trends in variation of pinnule morphology can be recorded.

Gondwana glossopterids. Due to fortunate fructification discoveries and cuticular studies it is now evident that this group is much more diversified than it was thought previously. Analyzing the distribution of morphological and epidermal features one can see here the same picture as was shown in above groups, viz. a limited set of features and their feeble correlation with each other.

Within the genera *Glossopteris* and *Gangamopteris* several generalized epidermal types have been recorded (SURANGE & SRIVASTAVA, 1955) some of them being characteristic of species of both genera. These genera also intergrade regarding the degree of midrib development. Some *Gangamopteris* species have rather few anastomoses. Through such species this genus can be morphologically connected with *Rubidgea*. The latter lacks anastomoses but its veins often bend and in some places nearly come into contact (*R. ovata* Maithy). In its vein and axial zone structure *R. ovata* is similar to *Gangamopteris intermedia* Maithy.

There are two main types of reticulate venation of glossopterids. Like *Lonchopteris* (see above), anastomoses can only connect the lateral veins, which are easily traced through the lamina (*Glossopteris decipiens* Feistm., *G. taeniopteroides* Feistm., *Gangamopteris cyclopteroides* Feistm., a.o.), or can change the venation into regular network (*Glossopteris retifera* Feistm., *G. conspicua* Feistm., *Gangamopteris intermedia* Maithy, etc.). An inconstant feature of both *Glossopteris* and *Gangamopteris* is the presence of the interstitial fibres within meshes (*Glossopteris fibrosa* Pant, *Gangamopteris fibrosa* Maithy). Identical fibres were also recorded in *Rhabdotaenia* (PANT, 1958; PANT & VERMA, 1963). Outlines and cuticular structure of its leaves are comparable to those of some *Glossopteris*, *Gangamopteris* and *Palacovittaria*, that can be explained by the affinity of the parent plants. *Rhabdotaenia* leaves have been previously described as *Macrotlaeniopteris* or *Taeniopteris*, i.e. were linked to the quite another group of plants. This is not surprising, since *Rhabdotaenia*, having thick midrib, open venation and lateral veins oriented at the right angle to the midrib, is much closer morphologically to some cycadophytes than to typical glossopterids.

By analogy with *Ctenis* series, one can expect the pinnate leaves among glossopterids. Indeed, PANT and MEHRA (1963) described *Pteronilssonina gopalii* with large compound leaves and noted "general resemblance of their epidermal cells and stomatal apparatus with that of glossopterid leaves like *Rhabdotaenia harkini* Pant and *Glossopteris colpodes* Pant" (l. c., p. 131). The main macroscopic difference between *Rhabdotaenia* and *Pteronilssonina* is in simple leaves of the former genus, and compound ones in the latter. A seemingly important difference

of *Pteronilssonia* from typical glossopterids is also in its forked rachis. But Pant and Mehra noted that the fructifications of glossopterids have been borne on stalk arising from the midrib, which can be consequently considered as forked. The bifurcation of the midvein is known in *Belinghtfootia* (LACEY and HUARD-MOINE, 1967) and *Belemnopteris*. The latter genus has the reticulate venation, whereas that of the former genus is open. Both genera most likely belong to the glossopterids and add to morphological variety of the group.

Paragondwanidium series. This series, comprising *Paragondwanidium*, *Angaridium* and some *Sphenopteris*, is characteristic of the Middle-Upper Carboniferous and Lowermost Permian of Siberia and especially fully represented in Kuznetsk, Tunguska and Minusa basins. The series may be begun with *Angaridium mongolicum* Zal. having once-pinnate frond with wedge-shaped pinnules, sometimes bilobed. The degree of pinnule dissection increases in *A. sub-mongolicum* Neub. and further in *A. finale* Neub. Then these dissected pinnules lengthen and the frond becomes twice-pinnate rather than once-pinnate, e.g. in *A. potaninii* (Schmalh.) Zal. The latter species is very close to *Paragondwanidium petiolatum* (Neub.) S. Meyen (NEUBURG, 1948), which is, in turn, similar (especially in its holotype) to *P. sibiricum* (Petunn.) S. Meyen. In some specimens of *P. sibiricum* the pinnules are strongly lobed and appear like pinnae with basally fused pinnules. These specimens closely approximate *P. odontopteroides* (Zal.) S. Meyen, which was previously described as *Sphenopteris*, since its frond appears twice-pinnate. The extreme member of the series is *S. kumpanii* Neub., resemblance of which with *P. odontopteroides* has been noted by NEUBURG (1948, p. 101): "A more deep dissection resulting in independent segments-pinnules of *Sph. odontopteroides* might lead to the pinna type of *S. kumpanii* or, vice versa, a fusion of independent pinnules of the latter species might give lobed pinnules of *S. odontopteroides*. The venation is similar in general". I should add that the venation of the pinnules of *S. kumpanii* and that of the basal pinnules of *P. sibiricum* are practically identical. Therefore it seems reasonable to propose a new combination *Paragondwanidium kumpanii* (Neub.) S. Meyen.

Some other series with similar variation of features will be dealt with only briefly.

The most ancient series comprises Devonian *Eddyia* (with simple leaves), *Archeopteris* (with pinnate leaf-like organs with pinnules having dissected or entire margin) and *Svalbardia* (with strongly dissected leaf-like organs). The Gondwana Triassic Corystospermaceae (like Peltaspermaeae) show once-pinnate [*Dicroidium hughesii* (Feistm.) Goth.], forked [*D. odontopteroides* (Morris) Goth.], bipinnate [*D. feistmantelii* (Johnston) Goth.] and bipinnate with a forked rachis (*Hoegia papillata* Townrow) fronds. A transition from compound-pinnate to once-pinnate fronds was shown by DOLUDENKO (1969) with Jurassic *Pachypteris* (*Thinnfeldia*). More or less similar series can be outlined among bennettites, in which epidermally similar *Pterophyllum*, *Anomozamites* and *Nilssoniopteris* differ from each other mainly in leaf dissection. In the Carboniferous and Permian of Angaraland a series connecting once-pinnate *Angaropteridium* with compound-pinnate *Neuropteris* appears. In a single series can be settled Cathaysian gigantopterids (ASAMA, 1959, 1962), whose variation is similar to that in *Ctenis* series and peltasperms.

In the examples presented above the author followed the customary definitions of the leaf-genera though it may well be that in reality some of them should be united like *Pachypteris* and *Thinnfeldia* (DOLUDENKO, 1969). Living plant studies show that the features usually estimated by palaeobotanists as generic may be only of specific importance. For example extant *Asplenium* have both simple *Taeniopteris*-like and bipinnate leaves. In their discussion on the separation of *Glossopteris* and *Gangamopteris* PANT and SINGH (1968) have reminded Seward's notion, that in living genera of ferns like *Scolopendrium* the presence of a midrib is an inconstant feature within a genus.

Series of forms with parallel variation of features can be outlined among other groups of the higher fossil plants, but in those the variation is observed in other features. While the plants considered above show the parallel change of venation, leaf dissection, cuticular features and axis division, among the representatives of the articulates the parallelism can be traced in various outlines of the sheath and in other types of leaves fusion, different leaf apices (with mucro or without it) and different order of leaf dichotomizing (MEYEN, 1971). In the lepidophytes one can see an independent appearance and similar variation of the leaf abscission and leaf scar formation, more or less regular orthostychies, false whorls, outlines and sculpture of leaf cushions, bark relief between the cushions, etc. Parallel variation of spores and pollen in different systematical groups, including fossil ones, is considered by L. A. KUPRIANOVA (1969).

Thus, in usual concept of the parallelism in higher plants some modifications should be introduced. The parallelism is commonly illustrated with the examples of two kinds. In one case there are two or more phyletic lines, going independently, but in the same direction with similar change of features and with similar final forms. It is very suggestive in this respect the independent reduction of megaspore number in megasporangia and the formation of the seed-like structure in the lepidophytes (both arborescent,—*Lepidocarpon*, and herbaceous,—*Miadesmia*) and articulates (*Calanocarpon*). Analogous examples have been considered above under "type A". The parallelism of this type is usually illustrated with taxa of the supra-generic rank.

In the other case, a parallelism of infraspecific variability of different species or specific variation of different genera of a single family was demonstrated. Namely this type of the parallelism has served for revelation of Vavilov's law (see above) in the first turn. The manifestation of this type at the higher taxonomic level (some examples of which have been demonstrated above under "B"), has been analyzed in a much lesser extent, though some observations have been published by VAVILOV (1922) and a few other neobotanists. What is the main cause after all, that the recurrence of the morphological types (at least vegetative parts) in higher taxonomic groups has been mostly neglected by palaeobotanists and neobotanists?

The reasons seems to be as follows. Among the living higher plants (excepts for the bryophytes) only the angiosperms and, in a lesser extent, ferns show considerable variety in the morphology of vegetative parts. The articulates, lepidophytes, psilotes, ginkgos and chlamydosperms are represented by one or a few forms. The conifers and cycads are represented only by highly specialized types, showing a limited number of morphological types of sterile shoots. Likewise, certain types of the leaves or leafy shoots predominate in extinct plant groups. However "predominate" does not mean a monopoly. But for some reasons or the other this point has been neglected by many palaeobotanists. Therefore a practice arose to refer fern-like leaves to the ferns or pteridosperms (although they may be of cycadalean affinity), shoots with needle leaves were almost invariably included in the conifers (such leaves may also belong to the cordaites), palmate leaves were usually considered ginkgoalean, and simple leaves with reticulate venation were mostly ascribed to the glossopterids, etc.

The assumption, that to every group of the higher plants corresponds a certain type of foliage leaves, prevails in the taxonomical practice of many palaeobotanists. The discovery of groups like *czekanowskias* and *bennettites* with leaves of ginkgoalean and cycadalean appearance respectively, leads one to the conclusion, that one type of foliage leaves may be characteristic of more than one group, and the only conclusion has been drawn, namely, the corresponding plants are more or less closely related. If one came across a type of leaf which was alien to the group, it was considered as an exception or abnormality and was explained

with convergency, i.e. the adaptation to certain (I would say "uncertain") environmental conditions.

As it was shown above, more wide-spread application of the epidermal and other microscopic techniques as well as more complete investigation of reproductive organs and their relation to vegetative parts lead one to reconsider many systematical views. It has been proved that the combination of different morphological types of vegetative parts within large systematical groups is not an exception, but rather a rule. Among cycads forms with fernlike fronds (*Amdrupia* and *Zamiopsis*?) and simple leaves with anastomoses (*Anthrophyopsis*) have been recorded. On the other hand within the glossopterids, usually placed into the pteridosperms, *Taeniopteris*-like (*Rhabdotaenia*) and *Nilssonia*-like (*Pteronilssonia*) leaves have been found. We have learnt that multiveined large leaves were characteristic of several quite independent groups of the conifers (*Phylladoderma*, *Araucariodendron*, *Podozamites*, etc.). At the same time from the example of *Buriadia* one can see that needle leaves may not be characteristic of the conifers only. The recent investigations have shown that some preperms possessed leaves indistinguishable from those of the ferns (*Sermaya*, —EGGERT & DELEVORYAS, 1967; "*Pecopteris*" *feminaeformis*, —BARTHEL, 1968; etc.), that some leaves similar to ginkgoalean ones belong to progymnosperms (*Eddyia*—BECK, 1967) together with leaves more characteristic to the preperms and ferns. The analogous picture has been demonstrated in the distribution of the morphological types of microspores among systematical groups (e.g., the conifers and pteridosperms show several common types).

It seems, that unbiased reconsideration of the systematical position of the known fossil plants on the basis of careful study with modern methods will show the growing variety in different groups and, on the contrary, a fuller recurrence of the morphological types between the groups. The variety and reiteration of structures in systematical groups of course have limits (we do not know them). For example, the lepidophytes will hardly show leaves with reticulate venation; and the cycads certainly would not show needle leaves, concentrated in the spur shoots (brachyblasts). However, the presence of needle leaves among the cordaites is quite possible (if the conifers have two main types of leaves, why couldn't the cordaites?). Simple leaves with anastomoses may be awaited within the peltasperms and bennettites.

Similarly one can suggest that large groups typically having a single type of the microspores will in future show other types. For example, it may happen that some peltaspermaceous pteridosperms had not only colpate pollen (of *Ginkgocycadophytus* type), known in the Upper Triassic species *Lepidopteris ottonis* (Goepf.) Schimp. (TOWNROW, 1960), but also some other type of pollen. In favour of this suggestion are the following observations. In the copper slates (Kupferschiefer) of W. European Zechstein (the Upper Permian) *Lepidopteris martinsii* (Kurtze) Townrow is a rather common plant, whereas the findings of corresponding pollen (of *Ginkgocycadophytus* type) are extremely rare not only in the shales but also throughout the whole Zechstein section. Solitary known pollen grains of this type may also belong to the plants whose leaves are described in the literature as *Sphenobaiera* (GREBE & SCHWEITZER, 1962). The palynological assemblages obtained from the hand-specimens full of *Tatarina* leaves consist mostly of saccate pollen. The same pollen is often found adhered to the *Tatarina* cuticle. The latter genus (see above) is believed at present as belonging to the Peltaspermaceae on the basis of the cuticular features and obligate association with *Peltaspermum* discs having the same cuticular structure. Of course, one can suggest that these leaves and fructifications

**Buriadia* is usually considered a conifer. But PANT and NAUGHTAL (1967) have shown recently that its conifer-like twigs bear scattered ovules; so there are no grounds to retain the genus among coniferals.

belong to another gymnosperm group. But in this case we will have to conclude that the megasporangiate *Peltaspermum*-like discs and peltaspermaceous type of cuticle is characteristic of unrelated plants, so that the parallelism will be shown in the female reproductive organs. It should be reminded also, that *Plilozamites*, which seems to be related to Peltaspermaeae, shows saccate pollen.

POSSIBLE CAUSES OF PARALLELISM

In attempts to explain the parallelism in plants the investigators refer to both interior peculiarities of the plant organization and environmental influence. The preference was mainly given to the latter. For example, a striking parallelism in pollen and flower structure in different groups of the angiosperms is explained by LEPPIK (1969) and KUPRIANOVA (1969) due to adaptation to the entomogamy (i.e., external biotic factor). ASAMA (1959, 1962, 1966) ascribed a parallel reduction and leaf coherention of many Upper Palaeozoic plants with the climatic changes, i.e., abiotic factor. A replacement of the stelar cylinder to one side of the stem in various fossil plants (some *Lepidodendron* and pteridosperms) was explained due to lianas.

Whether these explanations are true or not for these cases, we do not know. But somehow or other the reference to environment alone does not explain, why in many groups of plants some externally very simple structures, well represented in other groups, have not appeared during hundreds of millions years. We do not see, e.g. sori and synangia in the lepidophytes, reticulate venation in the conifers and ginkgos (rare anastomoses in *Ginkgo biloba* have no significance here). Explaining many features of the certain group as results of environmental factors we often forget that in other representatives of the same or allied group, inhabiting the same environmental conditions for many millions of years, these features have not appeared. For example, in club-mosses, in spite of their unique antiquity, the species of the sections *Selago* and *Subselago* do not have the true strobili. Following the tradition to consider independent origin of terminal strobili of club-mosses, selaginellas and horse-tails as an adaptation to better protection of sporangia, it is rather difficult to explain why for more than 300 million years the club-mosses with strobili could not force out species with scattered sporangia.

If the parallelism is stimulated exclusively by external influence, one can hardly understand the recurrence of variability trends in quite different groups which lived in quite different conditions in various geological epochs. These and some other considerations lead one to suggest that the source of the parallelism may be not only in the environment (biotic or abiotic) but also in the inherent qualities of the plant body.

The distribution of series shown above (type B) on the time scale is rather suggestive in this respect. It is hard to interpret these series as phyletic sequences, because being arranged in the direction of increasing complexity or, on the contrary, of reduction of the leaf structure, they do not coincide with the sequence of the forms in the geological section in all the cases. Indeed, the oldest peltasperms (*Lepidopteris martinsii*, known from the Autunien, i.e., Lower Permian) have the twice-pinnate frond with the intermediate pinnules. The same type of the leaf structure crowns the evolution of the group (Rhaetic *Lepidopteris*). In the second half of the Upper Permian forms with the simple leaves predominate (*Tatarina*). Once-pinnate leaves (*Scytophyllum*) appear in the Middle (?)—Upper Triassic and disappear before Rhaetic. The distribution through the geological section of the members of *Ctenis* series is quite irregular. The series of the glossopterids is distributed in a very interesting pattern. At first (in pre-Glossopteris flora) leaves without both anastomoses and midvein

appear, then come those with anastomoses (*Gangamopteris*) and soon with midvein (*Glossopteris*), whereas forms without anastomoses are absent. Later leaves without anastomoses and midvein appear again, but of another type than previously (*Rubidgea*). Further forms with anastomoses and mostly with midvein prevail. In the end of the group development compound leaves with forked rachis and lack of anastomoses (*Pteronilssonia*), simple leaves without anastomoses and with strong midvein (*Rhabdotaenia*), lobed leaves with anastomoses and forked midvein (*Belemnopteris*), and simple leaves without anastomoses and rather short midvein (*Palaeovittaria*) appear.

The consideration of these and many other examples gives the impression, that the development of the leaf morphology did not proceed directly from forms of simple venation and/or dissection to more complicated morphological types, but in a more intricate way. A group begins with some ancient forms, which may be considered *a posteriori* more primitive, and then it gradually accumulates the whole set of features, simultaneously losing from time to time other ones so that some plants become similar in some respect to previous (ancestral) forms.

How can we co-ordinate this statement with classical views on organ morphogeny and with arbitrary ways of phyletic transformation by overtopping, planation, fusion, reduction and, incurvation (ZIMMERMANN, 1959)? Essential contradictions with these views can be escaped if all the enumerated types of transformation are considered real, but more or less reversible instead of going in one direction. It means that besides reduction we should also take into consideration expansion (widening) and multiplication (fasciation, polymerisation), besides the fusion-the segmentation (dissection), besides the incurvation-the straightening (rectification), etc. The partial reversibility of the transformations has been pointed out by STEBBINS (1950). The concept of reversibility of the morphogenic modi invariably leads to a revision of many general and particular phyletic views, but I shall not draw reader's further attention on the matter, since it is the subject of a separate paper.

If the plant evolution did go partly in this way, namely by original accumulation of certain potentialities and then by their switching from one to another, it becomes rather difficult to consider the environment the only formative factor. It seems likely that environment plays a role of the limiting factor, trigger and modifier in a greater extent than usually thought, and its role was far from leading in formation of many important peculiarities of the plant body. The parallel accumulation of certain morphological types in various groups and the appearance of forms with more perfect symmetry in the course of evolution suggest that there are some unknown internal stimulators of form transformations. It is possible that in the future the regularity of forms and their remarkable recurrence in various groups (together with a limited set of the types observed) will be expressed in concepts of the general crystallography, particular case of which will be usual crystallography of inanimate nature.

PARALLELISM AND FOSSIL PLANT SYSTEMATICS

Whether these suggestions on the causes of parallelism are correct or not, the very fact of the independent origin of similar individual organs, entire plants and the series of them in unrelated groups can be considered well established. Therefore it should be borne in mind in taxonomical treatment of plant fossils. The examples presented above convince that leaves with or without anastomoses, simple or pinnate, with or without midveins may belong to closely related plants. On the contrary, externally strikingly similar remains of vegetative (and sometime of fertile) parts, which were regarded as species of a single genus, in reality belong to different families, orders and even classes. The characters invariably

used by the palaeobotanists as more important (at least as generic ones) prove to be incon-
sistent and independently occurring in various groups, being of a different taxonomic value
from one group to another. Instead of an accurate coordination and constant value of cha-
racters we see their complex recombination and a feeble mutual correlation. So it becomes
very difficult to separate in the combinations observed the constant characters from the
variable ones, important from minor, and hence in many cases the separation of genera
becomes the matter of convention and convenience.

How can we systematize the plant fossils in these conditions to minimize the possibility
of confusion? It seems that the first and most important premise here is to refrain from
fixing a strict *a priori* of the taxonomical value of any character. The constant value of a
character is admissible or even necessary in artificial classifications, constructed according to
dichotomous key. But compiling a classification, approximating to the natural ones, i.e.,
reflecting not only a similarity, but also the relationship of the members, the taxonomical
value of most, if not all, features should be established in the course of the investigation,
instead of being fixed beforehand. This approach is put into practice as follows.

The systematizing of a group proceeds from minor taxa to major ones, i.e. at first species
are assorted, then genera and only after that one can judge about suprageneric groups.
Usually the investigation goes in reverse direction. Firstly palaeobotanists identify the
general affinities of a specimen then look for a suitable genus in the literature and only
after this begin to think about the species (is it new or previously known), every specimen
having been compared individually with published figures and descriptions.

Let us begin the acquaintance with the proposed taxonomical procedure with species.
The species in palaeobotany have no relation to biospecies and may be only morphological
ones, since palaeobotanist operates merely with a limited set of the morphological characters.
A single available criterion of the species delimitation in palaeobotany is an interruption
(hiatus) in the continuous sequence of the morphological types. Therefore the first task of the
palaeobotanist is to build such a sequence. On the basis of the material coming from a single
locality and layer, a series is built, the members of which differ from each other in characters
obviously insufficient for species delimitation. The extreme members of the series should be
connected by a quite gradual transition (shown e.g. with nomogram), so that to refer
them to different species becomes absolutely unwise (though sometimes these series prove to
unite several previously described species). Such series have been called "monotopic"
(MEYEN, 1966). If a suitable material is available, analogous series are constructed with
remains of the same type obtained from other beds and/or localities. As a result a totality
arises, further splitting of which, due to its continuity, is not wise at all. This totality is what
can be regarded as the palaeobotanical species (in what extent this totality corresponds to
living biospecies in any understanding is not known). After this one can analyze the distri-
bution of characters within the totality, constant (specific) and variable ones being more or
less maintained. Monotopic series permit to ascertain limits of the species variability and to
reveal the parallelism of variation in different species.

The next step is a construction of several such totalities for the flora involved (within
given area, province or another phytochoria). If the morphological variety of the group
under question is sufficient, it may be possible to outline the larger totality, members of which
are closer to each other than to those of any other totality. Step by step the analysis covers
the material from bigger and bigger territory and larger stratigraphical interval. As a result
several totalities in their coordination become evident. Only then we can estimate their
taxonomic rank, to decide what characters are of major taxonomical value and what are
of less importance. Often the result is that characters previously considered generic or higher

receive the specific rank or lower. And, on the contrary, the features completely ignored beforehand, acquire considerable taxonomical value. Simultaneously it becomes evident, which characters are native to certain groups and which ones vary in parallels in different groups.

Only after this it is reasonable to refer to series (but not to a single similar form) of other floras. It may happen in this case that separate members of series, belonging to different floras, are strikingly similar to each other (and were described in the literature under a common generic or even species name), whereas the series themselves are different enough. This situation suggests an external similarity rather than the close relationship of these seemingly common forms. Of course only careful study based on modern methods can make the situation clear, but the place of a possible pitfall is known already, and the main hazard has been left behind.

Now let us refer to some concrete examples. For a long time the systematics of Angara Upper Palaeozoic cordaitan leaves was based on morphological characters such as dimensions and outlines of the lamina, structure of the apex, density of veins and their degree of divergence. With introducing epidermal investigation and by the construction of monotopic series it has become evident (MEYEN, 1966) that externally indistinguishable leaves may belong to different genera (*Cordaites* and *Rufloria*), that the presence of false veins (interstitial fibres), served as a basis for the delimitation of *Cordaites* from "*Noeggerathiopsis*", may be a single character, distinguishing closely related species within both *Rufloria* and *Cordaites*, that in species of different genera and subgenera the variability of apex outlines and of other characters goes in parallel direction whereas the leaf base morphology is much more constant.

A construction of something similar to the monotopic series on the generic level has permitted to put together the genera *Scytophyllum*, *Lepidopteris* and *Tatarina*, whose attribution to the same family (Peltaspermae) is supported by fructification findings, as well as with epidermal characters and presence of transitional morphological types. Such features as leaf dissection and mode of venation have proved to be more variable, resulting morphological types being repeated in other groups. *Tatarina* leaves, e.g., are much closer morphologically to Gondwana *Palaeovittaria* and *Rubidgea* (possibly belonging to the glossopterids) than to other peltasperms. At the same time it becomes evident that many peltasperms are characterized by a remarkable thick cuticle and probably by considerable hypodermal tissue development, so that the veins on imprints are hardly traceable. In this feature, which has never been paid much attention to from the point of view of taxonomy, the peltasperms differ well from the corystosperms and, on the contrary, are closer to the Jurassic genus *Pachypteris* of unknown affinities.

Although separate members of Gondwana corystosperm series and northern peltasperm (and allied forms) series are very similar to each other (*Compsopteris adzvensis* Zal. from the Upper Permian of Petchora basin is so strikingly similar to Gondwana Triassic *Dicroidium hughesii* (Feistm.) Goth. that at first it was referred by Zalessky to the latter species), but the total series themselves differ from each other rather significantly. Among northern peltasperms and allied plants there are no unquestionable forms with forked rachis and leaves with the predominance of stomata with four subsidiary cells. At the same time the coherent leaves with pinnuloids, i.e. with persistent original venation, but fused pinnules (as in *Scytophyllum*), are not known among the corystosperms (though such fronds can be predicted among them by the analogy with northern peltasperms).

In the delimitation of the Euramerican arborescent lepidophyte genera much attention is paid to the relation of distances between the orthostichies and between the leaves in an

orthostichy. This is one of the characters distinguishing, e.g., different *Sigillaria* groups. By the construction of the monotopic series in the Angara Lower Carboniferous lepidophytes, externally similar to *Sigillaria*, it was shown that this relation is remarkably variable here even within one species. *Sigillaria*-like forms having regular and distant orthostichies grade into the forms whose orthostichies are so close, that the bark resembles more that of *Lepidodendron*, instead of *Sigillaria* (these lepidophytes from my collection are still to be described). Being treated with criteria, adopted in the Euramerian lepidophyte systematics, the members of the lepidophyte series would be distributed in quite unnatural way.

I am convinced that similar relations can be easily disclosed among the mio- and megaspores, especially after an appropriate revision of the taxa considered common to different phytochorias.

It is evident that the construction of the series makes the taxonomical work more laborious. Moreover it requires much fuller collections and well preserved specimens. This is, however, the only way to have the systematics, maximally approximating natural one, to avoid the misinterpretation due to the parallelism, and to attain a grouping of fossil plants, which may be used in stratigraphical, phytogeographical and phylogenetic generalizations with the utmost success.

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