

PALYNOLOGY, NOMENCLATURE AND TERMINOLOGY

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SUMMARY

Some of the basic concepts common to plant taxonomy, palaeobotany and palynology are discussed such as "taxon", "taxonomic categories", "genus and species concepts", as well as "organ and form genera". The development of the specifically palaeobotanical and palynological concepts of organ and form genera is briefly treated in the light of the shaping of palaeobotanical thought and methods since Adolphe Brongniart. The need for a single category of an artificial nature (i.e., form genus) is acknowledged; the need for a second category of such nature (i.e., organ genus) is questioned. The general guide lines for good palynological practice given by FAEGRI et al. (1950) are recommended for future use and are reprinted as an appendix to this paper.

INTRODUCTION

The organizers of the Second International Conference on Palynology (Utrecht, The Netherlands, 1966) have asked me to present a contribution on palynology, nomenclature and terminology. I do not know whether any of you have already had occasion to read the July 1966 issue of the journal *Taxon*, in which the neobotanist A. C. Smith formulates Smith's law. This law is as follows: the less responsibility one has for administering a human activity, the better qualified one is to give advice about it, a modern variation of "The best horseman is always on his feet". It is no doubt out of respect for this law that I have been asked to contribute, since what I know about palynology is negligible, so that I seem to be quite well qualified to give you advice. However, in view of the fact that in the past two decades I have had something to do with botanical nomenclature, and even with botanical terminology, you will perhaps permit me, despite your president's disregard of Smith's law, to look at some palynological publications with the eye of, let us say, a nomenclaturist or a general taxonomist.

It is doubtful actually, whether there is any such thing as a nomenclaturist,

because botanical nomenclature is nothing by itself. It is a system of practical agreements which enables us to understand and discuss each other's taxonomic concepts. Nomenclature makes taxonomic discussion possible, because it provides a common meeting ground. It is just one of the aspects of the language of taxonomy, and it is nothing if dissociated from our science.

TAXA AND CATEGORIES

Before I start talking about nomenclature and terminology, I think I should make it clear what I mean by taxonomy, and more especially, since taxonomy is the scientific recognition and treatment of taxa, what I mean by taxon. It has struck me that in some palaeobotanical and palynological publications this term is used in an absolutely incorrect manner. Sometimes we read "the taxon organ-genus" or "the taxon species". This usage is entirely at variance with the originally intended meaning of the term, which is stated in the *International Code of Botanical Nomenclature*. The term was introduced by my countryman and colleague, H. J. Lam, the nestor of Dutch plant taxonomy, to replace the term "taxonomic group of any rank". It refers ultimately to an assemblage of individual plants. Such an assemblage or group may constitute a recognizable unit in an evolutionary system, but it also constitutes any group of individuals brought together by the systematist because he considers them to be related in one way or another. *Ranunculus acris* is therefore a taxon. This taxon has the rank of species. The genus *Ranunculus* is a taxon, of the rank of genus. The abstract concepts "species" and "genus" are categories. These categories are, in the sense of Kant, a-priori concepts by which we can understand or classify matter. The categories used in taxonomy have a hierarchic order: form, variety, species, genus, family, etc.

I do not want to offend you with this elementary dissertation, but this definition of taxon has some bearing on what I should like to say with respect to those typical palaeobotanical and palynological phenomena called "organ genera" and "form genera".

SPECIES AND GENUS CONCEPTS

Another very important issue to determine before discussing organ genera and form genera are the questions: what is a species, what is a genus? Are the criteria which define these categories the same for neobotanists, palaeontologists and palynologists? We might also ask, perhaps, are they the same among palynologists? I shall not try to answer this question in any detail; that would lead us much too far. The answer to the question "Is there one species or genus concept, or are there more?" is, obviously, "there are many". I shall not even enumerate them, but

for the species concept I can refer to the modern "biospecies", which is an ecological-statistical polytypic concept with the population as the basic unit; in other words, an interbreeding or potentially interbreeding group of populations. Modifications of this biospecies concept occur when one brings in the time factor; some modern zoological taxonomists speak then of chronospecies. This concept of a species with a high reality-content and as a concrete, finite entity is clearly in contrast with the older, more familiar, non-dimensional, typological concept of the morphospecies. Here a species is an assemblage of individuals sharing certain morphological characteristics. The type specimen of the species is like a single fixed star in a galaxy. Of necessity the palynological species concept is usually that of the morphospecies, typological rather than biological, non-dimensional rather than finite. This difference in species concepts is often offered as one of the main reasons why palynologists and palaeobotanists on the one hand and neobotanists on the other speak different languages. Nothing could be farther from the truth: most present-day work in taxonomic neobotany has the "morphospecies" of necessity as its basic concept. Think only of all those studies which must necessarily be done on the basis of herbarium specimens; and after all, what are herbarium specimens other than man-made sub-fossils? Notwithstanding the great theoretical possibilities of working with living plants, much of the taxonomy of today's neobotanists differs only in degree from that of the palaeobotanist: both are working with dead material, both are often dealing with fragments only.

The differences in the generic concepts are far less pronounced. So far, experimental taxonomy has made very little headway towards a biological genus concept. I quote ROLLINS (1953), one of our foremost experimental taxonomists: "Ordinarily, cytogenetic approaches will not provide the broad general outlines of classification within a genus, nor is it expected that given genera will always be sharply delimited by the use of cytogenetic criteria alone . . ." In short, the neobotanist's generic concept is typological and non-dimensional: that of a type (a species) with a galaxy of other species around it, bound together in the mind of the observer by formal relationships. It is clear that here the basic concepts of palaeo- and neobotanists are identical in principle.

Granted, however, the many diverse opinions, delimitations and especially philosophies among ourselves, there is at least one basic common meeting ground: botanical nomenclature. Whatever our species concept, whatever the nature (concrete or abstract) of our species, we must follow the same rules in naming them. The same is true of genera and categories of other rank. The strongest common link we have between our diverging and often conflicting taxonomic opinions is our use of a single system of naming our spiritual children: botanical nomenclature.

Ever since I first became involved in the editing of the *International Code of Botanical Nomenclature*, shortly after the Stockholm Congress of 1950, I have been puzzled by the special entries concerning fossil plants, and more specifically by the provision concerning organ genera and form genera. Allow me to quote the relevant part of the Code:

“Since the names of species, and consequently of many higher taxa, of fossil plants are usually based on fragmentary specimens, and since the connection between these specimens can only rarely be proved, organ-genera (*organo-genera*) and form-genera (*forma-genera*) are distinguished as taxa within which species may be recognized.

“An *organ-genus* is a genus assignable to a family. A *form-genus* is a genus unassignable to a family, but it may be referable to a taxon of higher rank. Form-genera are artificial in varying degree”.

This looks all very nice and simple. It is evident that spores and pollen grains, being after all “fragments” of a special kind, will very often not show sufficient characteristics to guarantee recognition of taxonomic or phyletic relationships. They have to be dealt with, and the best way to do this is to accept the artificial nature of the classification one is able to make. This is not limited to fossils. A similar situation is found with imperfect fungi, many of which never show the perfect state (sexual reproduction), and of which the natural affinities cannot be established either, so long as they remain in the imperfect stage. Such a genus *may* be perfectly natural, and all the plants brought under it *may* eventually be shown to have comparable perfect states, but it may also be different. In other cases, wood anatomists have to identify wood samples unaccompanied by voucher specimens carrying flowers and leaves, and ecologists must identify sterile grasses or sedges. All these problems are related and come back to one single question: are the characters shown by the fragment such that we can recognize the whole plant from the fragment? In the case of many fossil spores and pollen grains, we shall obviously never know. With recent plants we shall ultimately know; with fossil plants this will be the case only in a very restricted number of cases.

The thing that puzzled me about these special categories, therefore, was not that they existed, but simply that there were two! What is actually the difference between them? The Code gives what seems to be a simple answer: if the fragments are such that the genus can be brought to a family (obviously meaning a family in the natural system, or phyletic system if you like) it is an organ genus. A form genus, on the contrary, is unassignable to a family: “form-genera are artificial in varying degree”. By implication, organ genera are ‘natural’. One must always be very careful with the use of the term ‘natural’, but what is evidently meant here is a classification based upon a knowledge of the complete plant and making use of a great number of characters.

We may, therefore, define the concept form genus as follows:

"A form genus is a genus of fossil plants of which only relatively small but comparable parts are known (e.g., spores, pollen grains, fruits, leaf impressions). If the connections between these parts and the complete individual plants become known, the species of a form genus may have to be considered as belonging to entirely different genera which need not even belong to the same family, order or class. Form genera are therefore by definition artificial." You will notice that I left out the statement about form genera not being assignable to a family. For the moment, however, we should leave this in, because it is in the Code, but I have a special reason for saying it in a different way.

However, what are organ genera? Yes I know, you will at once say: "*Lepidocarpon*", or "*Cupressacites*". I do not know whether I can go along with you here. I have tried to trace in the literature the history of these concepts, with the very capable assistance of my friend Dr. J. M. Schopf. Let us turn back for a moment to the birth of modern palaeobotany, which took place between 1820 and 1830.

BRONGNIART'S PALAEOBOTANICAL PRINCIPLES

The first author to formulate certain fundamental general concepts and to apply them to the multitude of fossil plants thus far known, was that remarkable genius and many-sided botanist, Adolphe Brongniart (1801–1876). He did not confine himself to the description of the fossils, but also provided a very clear methodological and theoretical basis for palaeobotany. The principles formulated by him had been only hesitantly and vaguely expressed by others, and vagueness was foreign to the fine Cartesian spirit of Adolphe Brongniart. I cannot dwell upon this subject, much as I should like to, but I want to call to your attention that Brongniart adopted three basic tenets which can be designated as the taxonomic, the stratigraphic and the floristic principles.

The taxonomic principle is the one that interests us specifically at this time. It states that fossil plants have to be studied as such and are not necessarily remains of species with living representatives. In many instances, said Brongniart, the fossil remains are fragments of plants; the connection between the various organs is often unknown. Each fossil has to be described as such. The characters must be directly derived from observation and not from speculative implication of relationship with other plants. One has to stick to the clearly visible characters and not confuse observation, interpretation and taxonomic belief. It might then become possible to recognize the fossil remains as representing present-day plants, but it might just as well be that no links with better known recent plants could be established. The concept of form genera was also first formulated by Brongniart (without using this term, of course) when he stressed the fact that it is better to have an artificial classification based upon a restricted number of characters derived

from similar fragments, than to speculate too soon upon natural relationships. For example, Brongniart's division of the ancient "taxon" *Filicitis* into *Sphenopteris*, *Neuropteris*, *Pecopteris* and, e.g., *Odontopteris* is an illustration of this procedure. This subdivision was based on the patterns of the nerves of fragments of the fronds. Brongniart stressed, however, that it should always be the aim of the palaeobotanist to try to find the "natural classification". To this end it was necessary to use all possible approaches, not the least of which is anatomy.

I shall not discuss in any detail the other two principles, the stratigraphic and the floristic. Brongniart was the first to state clearly that plant fossils could be used for stratigraphic purposes. The influence of his father, the famous palaeontologist Alexandre Brongniart, and that of the founder of stratigraphical geology, William Smith, is evident here. The floristic principle is an elaboration of the stratigraphic principle: just as individual fossil species can be characteristic of individual strata, so can floras, or combinations of species be characteristic of geological periods.

These basic statements of palaeobotanical methodology are still perfectly valid today.

Palaeobotany evolved quite happily along these lines until the turn of century. Men like Lindley and Saporta, and many others, worked in full agreement with the basic methods outlined by Brongniart. It was generally admitted that many genera and species of fossil plants were artificial, but nobody bothered to set up a separate hierarchical classification with its own terminology for them. Ultimately, of course, the aim was to find the "natural" niche for each of them.

With the increasing knowledge of forms and refinement of techniques, however, the awareness of the formidable difficulties became such that the palaeobotanists were forced to create more categories. The English anatomical school of palaeobotanists around Scott and Seward developed the concept of organ genus as a genus of fossil plants based upon the characteristics of one particular organ, of which the significance was such, however, that it was always possible to place the genus in a natural family. At the International Botanical Congress, held in Amsterdam in 1935, the British palaeobotanists presented a motion to lay down rules for "organ genera and artificial genera of fossil plants", whereas Jongmans, Halle, and Gothan proposed the adoption of *combination genera* in those cases where the organ genera were found to have been based on parts of the same plant.

The British proposal was accepted in principle, and the concept of combination genera was rejected. No firm decision was taken, however, and the palaeobotanical rules of the Amsterdam Congress were never published except in unofficial form. The Stockholm Botanical Congress of 1950 took up the subject and laid down the rule as it now stands. A group of American palaeobotanists had submitted a set of proposals which resulted in considerable clarification. The concepts organ and form genera were kept, and it was stressed that the naming of all fossil taxa, whether artificial or natural, was subject to the type method.

Combination genera were no longer spoken of; on the contrary, with the consistent application of the type method it became much simpler to follow the main rule of priority.

The rules as adopted by the Stockholm Congress made it clear that the word "taxon" could be applied to both natural and artificial groups of plants. This was an important clarification: a taxon is an assemblage of individuals considered related for taxonomic purposes (directly or indirectly via taxa of lower rank). Taxa have names, and these names are linked with types. For nomenclatural purposes it is possible to say that a species is a number of individuals grouped around a type specimen. It should again be stressed, however, that this does not mean that the rules of nomenclature interfere with taxonomy. The various species concepts remain applicable. It is only for the purpose of naming, and thereby attaining mutual understanding, that we need the purely pragmatic type-method of the Code.

THE BROMMA RESOLUTION

Some of you may recall that a palynological meeting was held at Stockholm (Bromma), on 11 July 1950. Palynology had come into its own, and the knowledge of fossil and recent miospores had grown into the flourishing science of today. Since many palynologists are not biologists by training and come from the ranks of stratigraphical geology, for example, it is understandable that the use made of the various biological concepts is not always the same. A resolution adopted at Bromma and worked out by Faegri, Potonié, Selling, Erdtman and Schopf made it clear that for formal taxonomic classification, palynologists should regard fossil or sub-fossil pollen grains or spores as representative of form genera or form species (FAEGRI et al., 1950). The group echoed the explicit instruction that "if pollen grains or spores show characters restricted to one species of the modern flora, identification should be made with the modern species and genus".

Other useful and logical instructions were given, and it would seem that on the whole most of them have been followed by palynologists. In some instances, however, I have my doubts. First, there is the interesting circumstance that in this resolution no mention is made of organ genera. This does not mean, however, that we do not find organ genera in the palynological literature since 1950. The reason for this is the statement in the Code that organ genera *are* and that form genera *are not* assignable to a (natural) family. I think this is an unnecessary complication. The genus *Cupressacites*, if I understand the Russian publication of 1960 correctly, is certainly assignable to a family, but the pollen grains of the genera of that family are practically indistinguishable from each other. For that reason it is necessary to have an artificial genus, which really does not differ in principle from other such genera where the degree of artificiality is just

a little higher. Obviously, then, there is no need here for a second concept.

The number of known fossil miospores has now become so enormous that palynologists have found it necessary to have not only form genera and form species, but also higher categories, to classify their units.

At this point I can refer to the system developed by Potonié, with the categories anteturma, turma, subturma and infraturma. The category below infraturma is then the form genus. There is a great advantage in this terminology of categories: they do not remind one of the commonly adopted categories of the phyletic system. One of the weaknesses of the term form genus is that it has the word "genus" in it. This weakness is unavoidable because of the necessary integration of the artificial classification into our system of nomenclature. From a methodological point of view, however, the question whether a form genus is equivalent to a genus is just as irrelevant as the question whether the categories of the Linnaean artificial system such as Triandria, Tetrandria and Hexandria are families or orders.

NOMENCLATURE AND TERMINOLOGY IN PALYNOLOGY

There is one other phenomenon in palynological nomenclature which has struck me. Some of the form genera are so extremely artificial that, in my opinion, they entirely lose the character of a taxonomic concept and become a terminological concept instead. In taxonomy we deal with groups of plants related in some particular respect. In terminology we deal with isolated morphological, physiological, genetical, or other phenomena which are in principle completely independent of any taxa. The terms describe, for instance, morphological characteristics; the taxa group individual plants or fragments of plants.

Turning now to the diagnosis of the form genus *Fenestrites* we find:

"pollen grains provided with pseudo-pores, lacunas (fenestrate)". This, in my opinion, is the definition of the term "fenestrate" and nothing else. Pollen grains which show this characteristic are just "fenestrate", that is all. Why burden nomenclature with another name for this? When I then read that "the type-specimen [of the type species *Fenestrites spinosus*] is a recent pollen grain of *Crepis paludosa* MOENCH", a composite, with age and locality "recent, Holland" I am completely lost. I can understand the reason why the author does this, but I cannot admire it. What he really does here is to explain the significance of a term by pointing at a recent pollen grain. Surely this is not taxonomy, but pure terminology, and it is much better to explain what *fenestrate* means in the way of KREMP (1965). Under the *International Code of Botanical Nomenclature* the name *Fenestrites spinosus* is illegitimate in any case, because it is a superfluous name, so we need not worry unduly. However, this is not an example to be followed.

On the other hand, I must say that I have the impression that this is perhaps

a somewhat isolated case. You will know this better than I do. My point here is that the more artificial and specialized your form genera become, the more their character becomes terminological rather than taxonomic.

Now a final word about the organ genera. I should think that this category could disappear from the Code without any harm. After all, we have the possibility for a conventional system of nomenclature for fragments and isolated spores in the form genera, form species and the further system developed by Potonié.

The whole question of organ genera is that of the "pars pro toto": Can we take the part for the whole? Can we assume that the organ which we describe shows sufficient characteristics to ensure that our taxonomic unit would stand if the entire plant were known? Now let us not forget that in neobotany we do much the same. We describe numerous species and genera on the basis of sub-fossil fragments called herbarium specimens. True, in most cases these herbarium specimens will show more organs and more characteristics than most fossil specimens. But even so we know nothing about the stem or the roots, or about the leaves on sterile branches of many tropical trees known only from one or two small branches with some flowers. Yet the neo-taxonomist assumes that he can take the part for the whole. Taxonomy is almost always a question of evaluation of incomplete material, and palaeo-taxonomy does not differ in any fundamental way. In this connection, it might be said that many of the genera and species described by neobotanists only on the basis of herbarium specimens come very close to being organ genera or organ species. The difference really does not lie in the nature of the material, fossil or recent, but in the species concept of the author. Perhaps I should say: "in the species concept the author is in a position to use". The bio-species and bio-genera may occur almost exclusively with neobotanists; the so-called organ genera and species are used by neo-botanists and palaeobotanists alike when they use the common morphological, non-dimensional species concept. This is one more reason why organ genera are hardly needed: when a palaeo-taxonomist is convinced of the natural affinity of the taxon he describes, down to the level of family, genus or species, and if this affinity is to extant genera, he should follow the *International Code of Botanical Nomenclature* and refer them to these genera. In such cases there is no need for a separate nomenclatorial system; such names will not even be acceptable under the Code. I need not emphasize that the *International Code of Botanical Nomenclature* applies to all taxa, whether recent or fossil. Special nomenclature is admitted only as a matter of convenience, to admit the classification of objects with insufficient characteristics to relate them to taxa of the natural system, whether recent or fossil!

As soon as the mycologist realizes that he is dealing with an imperfect fungus, he will establish an artificial taxon, because he knows that he cannot take the part for the whole. In palaeobotany, as in palynology, you need only one possibility, and not two or three, when dealing with specimens which you know or which you assume are not representative of the whole plant. This possibility

is that of the form genera and species. Most organ genera of palaeobotany are in fact just ordinary genera which have a place in the natural or phyletic system. Others are nothing but form genera.

I may perhaps end with two suggestions. First, I think I ought to make a plea that the *International Code of Botanical Nomenclature* be faithfully followed by palynologists. I know that in most instances this is done, but even in very recent literature one can find examples of unwarranted changes of names, disrespect of the rule of priority, incorrect retypification, adherence to page-priority and the like. I do not want to enter into all of this because it is likely that there is only a small minority of offenders. I think that under the present Code, and especially if one follows the guide lines given by FAEGRI et al. (1950) (reprinted here as an appendix), one has an excellent instrument for mutual understanding. Such mutual understanding eliminates the risk of confusion and works towards our common ideal of an internationally integrated science.

Finally, I should like to suggest that at the next international conference on palynology you devote a special symposium to these questions of species and generic concepts, and to the role of nomenclature and terminology in making them understood. I sometimes have the feeling that we botanists are less conscious of the need to discuss the fundamental principles of our science than the zoologists and palaeontologists are, and this (I am sure you will agree with me here) is an undesirable situation!

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APPENDIX

SUGGESTIONS FOR STUDENTS OF PLANT MICROFOSSILS¹

(1) Whenever formal taxonomic classification of fossil and sub-fossil pollen grains and spores is desirable or necessary, palynologists should regard them as representative of form genera or form species in the sense of taxa according to the *International Rules of Botanical Nomenclature*. Nomenclatural types should be designated wherever the Rules require it.

(2) In cases of uncertain identification it is often preferable to propose new artificial taxa rather than to apply old names in a loose or inexact sense conducive to confusion.

(3) If pollen grains or spores show characters restricted to one species of the modern flora, identification should be made with the modern species and genus.

(4) It is desirable to describe and illustrate spores or pollen grains of the living species whenever fossil spores or pollen grains are first identified with it. If the modern forms are already described and illustrated, references should be given.

(5) If pollen grain or spore characters are not restricted to a single modern species, identification with a modern species is always to be avoided.

(6) If pollen grain and spore characters are restricted to a group of species included in a modern genus, the name of the subgeneric group or other indication of the group of species should be given (e.g., *Coprosma*, aff. *C. propinqua* group).

(7) If pollen grain or spore characters are similar within a modern genus, fossil spores or pollen grains may be identified with the genus, but an inclusive form species may need to be established.

(8) If the above procedures are not applicable, fossil pollen grains or spores may be used as a basis for establishing new form genera in accordance with the Rules.

(9) If form genera are resorted to, an author should indicate the smallest taxonomic subdivision of the plant kingdom to which they can be consistently referred.

¹ Resolution adopted by the Palynological Meeting, held at the Technical High School in Bromma, Sweden, Thursday afternoon, July 11, 1950. This draft has been rearranged by J. M. S. (7-13-50), from the original rough draft, as adopted, which was worked out by Faegri, Potonié, Selling, Erdtman, and Schopf during a recess in the Palynological meeting.