

IMPORTANCE OF UNDERSTANDING OF THE ARCHITECTURE OF FROND FOR SYSTEMATICS OF NEUROPTERIDAE AND CALLIPTERIDIACEAE AND ITS STRATIGRAPHIC IMPLICATIONS

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The "Pteridophylla" have been originally distributed into groups defined by the general outline and the venation of the ultimate foliar elements (=pinnules). However, since the works of Grand'Eury, Stur, Zeiller, the frond architecture is taken more and more into account to settle the relationships between the major groups of Pteridospermophyta (=Cycadofilicophyta), the anatomical information and the knowledge on the reproductive organs remaining rather poor and clearly insufficient as compared to the amount of the known impression-compression foliage.

The genus *Neuropteris* is one of the most ancient genera established, it was created by Brongniart in 1822 as a section (=subgenus) of the genus *Filicites* and was characterized by the oval or rounded outline of the pinnules, not attached to the rachis by their whole base, the nervules of which were distinct, dichotomous and rising from the point of insertion of the pinnule to the rachis.

The numerous studies of the second half of the XIXth and of the first half of the XXth centuries have progressively improved a two-fold classification of Neuropteridae:

— Imparipinnatae and Paripinnatae of Gothan, terms established from the characters of the apex of ultimate pinnae,

— Whittleseyinae and Potonieinae of Halle, taking in account what was known about the reproductive male organs,

— Cyclopteridaceae and Rachivestitaceae of Corsin and Bertrand, using such criteria as, respectively, the presence or absence of *Cyclopteris* at the base of the frond on one hand and, on the

other hand, the lack or presence of intercalary pinnules on the main rachides, all these terms were, for the cited authors, more or less equivalent and corresponding to one and same subdivision of the group Neuropteridae.

In fact the precise study of the architectural mode of the building of the frond, and a critical study of the criteria used by the preceding authors, show that there are three main lineages within the Neuropteridae. It was the presentment of Gothan in 1913, when he divided his group of Imparipinnatae into Imparipinnatae communes and Imparipinnatae intercalatae, taking into account the lack or the presence of intercalary pinnae on the main rachides, but, later on, he did not think that it was useful to maintain such a distinction.

The first of these lineages is that of *Neuralesospermae* which comprises, among the Neuropteridae, the species belonging to the *Neuralesospermae schlehani* Stur group, which are strictly related to *Alethopteris*. That lineage is characterized by the existence of a frond strictly pinnatifid. It must be noted that these plants, if they have imparipinnate last order pinnae, are devoid of *Cyclopteris* (and also intercalary pinnae) and, consequently, on the contrary of what P. Corsin thought, the term Cyclopteridaceae is not equivalent of Imparipinnatae. Furthermore, a critical study of the published data shows that it is only with the species belonging to this group that have been found reproductive male organs of *Whittlesey* type and, thereby, the term Whittleseyinae cannot be applied to the whole group Imparipinnatae.

The second lineage is the *Parispermae* one. It

comprises the species of the genera *Paripteris* Gothan and *Linopteris* Presl. The characters of the frond in that group are very clearly defined. The architecture of the frond is of a sympodial dichotomous type; the frond is built by successive unequal dichotomies of a fundamental rachis (Phyllopodium of Bower) bearing entire pinnules, attached to a point and never lobed. There is not at all any laminar lobation nor segmentation, all the rachides, what their order may be, are in fact strictly homologous and all bear similar pinnules. The ultimate pinnae are paripinnate, i.e. they are ending with two pinnules of smaller size than the adjacent pinnules. The male reproductive organs are of *Potoniaea* Zeiller type.

The third lineage is the Neurodontospermae one. It assembles at least the following genera: *Neuropteris* s.s. *Reticulopteris* Gothan and *Odontopteris* Brongniart. The frond in this group corresponds to sympodial dichotomous subdivisions of a phyllopodium bearing last order (=ultimate) pinnules. Compared to the frond of the preceding lineage, there has been a laminar segmentation at least of one order; the existence of such a phenomenon explains the fact that the ultimate pinnae are imparipinnate, and that the intercalary elements are last order pinnae, except for certain species with big "pinnules" (*N. scheuchzeri*, *N. macrophylla* for instance) where the laminar segmentation becomes less pronounced, the last order pinnae show a tendency to stay at the stage of big "pinnules", some of which have an intercalary position. This implied that the term "Rachivestitaceae" is not satisfactory because it could be applied either to these last species cited, which are nevertheless imparipinnate, or to the various species of Parispermae.

The architecture of the Neuropteridae's frond makes very easy the understanding of the architecture of the Callipteridiaceae (=Callispermae) frond, and at the same time allows the deduction of the general evolution inside this phylum and gives precisions about the characters of the fronds that their ancestors should express.

The genus *Callipteridium* Weiss 1870, abundant during Stephanian times, is characterized by

somewhat falciform pinnules attached to all their base on the rachis; this fact explains why this genus has very often been linked with the Alethopteridae. It would be also characterized by the presence of intercalary pinnules on the rachides of penultimate order and intercalary pinnae or the main rachis of the frond.

In R. H. Wagner's sense, there would have been an evolution from a *Praecallipteridium* subgenus (corresponding to P. Bertrand's genus *Pecopteridium*) to a *Eucallipteridium* subgenus by progressive acquisition during Stephanian time, of intercalary pinnules, first appearing near the apex of the penultimate rachides and progressively moving down the frond. These intercalary pinnules, in Wagner's sense, would have nothing in common with the intercalary pinnae present on the main rachis of the frond. We are going to see what can be said about such assertions.

In fact the observation of the structure of the fronds in the genus *Palaeoweichselia* or in the subgenus *Praecallipteridium* shows that they are built in the same way as the fronds of the Neurodontospermae; the fundamental element is here also a phyllopodium, bearing last order pinnae, which divides itself in a dichotomous manner, and by the way, the "created" intercalary elements are pinnae of last order. The examination of various specimens gives the key to understand the way by which one can pass from the *Praecallipteridium* stage to the *Eucallipteridium* stage. It becomes easy to see that, in the genus *Callipteridium* sensu lato, intercalary pinnae and intercalary pinnules are in fact homologous elements, the intercalary pinnules correspond simply to intercalary pinnae which became less and less differentiated, because of the phenomenon of reduction in size which has affected the frond of the plants of that time, in response to the climatic evolution. The *Eucallipteridium* stage can be deduced from the *Praecallipteridium* stage by reduction of one degree of the laminar segmentation, reduction which has started, of course, at the extremities of the lateral ramifications of the frond. The reduction becoming more important, one can even arrive to the *Callipteris* stage, in which the intercalary elements can

be only intercalary lobes or may completely disappear.

So, from upper Westphalian to Permian, there is a general tendency to a reduction in the size of the frond. If we extrapolate the argument on the reverse way, we could suppose that the direct ancestors may have had a frond with more divided laminar elements.

A critical study of all the specimens found in the Sarre-Lorraine and Northern France Coal basins leads to the conclusion that all the previously cited of *Pecopteridium* and *Praecallipteridium* from Northern France Coal basin and Sarre-Lorraine Coal basin below the level of tonstein 100 belong to *Palaeoweichselia defrancei* Brongniart. A precise stratigraphic study has also led to the conclusion that, in Sarre-Lorraine Coalfield, the extinction of *Margaritopteris coemansi* (Andrae) occurs just below the level of tonstein 60 and that it is over that precise level that *Callipteridium* (*Praecallipteridium*) *jongmansii* P. Bertrand can be found. The gathering of numerous specimens has allowed to show the striking similarities which exist between these species and, in 1977, we made the hypothesis that *Margaritopteris coemansi* (Andrae) was the direct ancestor of *Callipteridium jongmansii* and of *C. armasi*, *M. coemansi* being once more divided at the laminar level, and if this hypothesis was true, the fronds of this last species had to combine the following characters:

- 1) The ramification ought to be of a sympodial dichotomous type,
- 2) The fundamental laminar elements born by the phyllopodium had to be more or less tripinnatifid elements,
- 3) The intercalary elements consequently were also more or less tripinnatifid elements.

Till that time only one specimen of *Margaritopteris coemansi*, figured by H. Potonie, could support point 1, but was not enough complete to give a verification about points 2 and 3. We had the chance to collect in 1976 some specimens of *Margaritopteris conwayi* (Lindley and Hutton) [posterior synonyms: *Margaritopteris pseudocoemansi* Gothan = *Pecopteris vedrinei* Dalinval] which showed the rightness of the proposed hypo-

thesis and which allowed us to set at least in upper Namurian the origin of Callipteridiaceae, but we are pretty sure that this lineage is still more ancient, due to the fact that a species created by Purkynova in 1970 and designated under the name *Neuropteris multivenosa*, from the lower Namurian, belongs certainly to that lineage.

The comparison between *Margaritopteris conwayi* (Westphalian A—lower Westphalian C) and *Margaritopteris coemansi* (lower Westphalian C) shows that the maximum stage of laminar segmentation is reached by *M. coemansi*, and, with *M. conwayi*, we are getting down the curve of the laminar segmentation through the time. If we extrapolate this last tendency of the Namurian, the fundamental laminar element in the species *N. multivenosa* should be a little less divided than in *M. conwayi* and should be at the stage of a more or less bipinnatifid pinna. If that point could be confirmed in the future, this would bring a supplementary argument to the hypothesis I had formulated in 1967, that is that the origin of the diverse lineages we have dealt with in this paper would have to be looked for among Dinantian plants with a foliage at the "cyclopteridian stage", somewhat similar, for instance, to the foliage of the genus *Cardiopteris* Schimper (= *Fryopsis* Wolfe). In a stratigraphic point of view, the revision of the various species has permitted to prove the existence, in the Northern France Coal basin, of strata of lower Westphalian D stage, and to correct the signification and the extension of the Westphalian D stage for the Sarre-Lorraine Coalfield, where the concept of Westphalian D had been defined originally, but there is another point which is worthwhile to be mentioned, in the circumstances the stratigraphic use of certain morphological characters. So, in the case that was given the postulate that the acquisition, in the genus *Callipteridium*, of intercalary pinnules from the top to the basis of the frond, between last order pinnae, was gained gradually during lower and middle Stephanian times, any frond of specimen showing clearly intercalary pinnules gave automatically a Stephanian age to the corresponding strata. But such an argument, applied in a too rigid

manner, would lead to important stratigraphic mistakes. On the reverse, when one has understood that intercalary pinnules and intercalary pinnae are strictly homologous elements which exist "originally" in the whole frond, due to the sympodial dichotomous mode of "branching", it is clear, that the argument "presence of intercalary pinnules" can only be used on "statistical" grounds.

At the evidence, due to the reduction in size of the fronds during Stephanian times, it is clear that one will find more often in Stephanian strata specimens with intercalary pinnules than in Westphalian strata. It must be said, however, that intercalary pinnules exist in the subgenus *Praecallipteridium* near the top of the lateral ramifications

during upper Westphalian times, and, on the reverse hand, fossils belonging to the subgenus *Eucallipteridium* and found in Stephanian strata may be devoid of intercalary pinnules; all these facts can only be explained under the consideration of the frond architecture.

In conclusion, all these considerations show clearly that the understanding of the mode of frond architecture is a fundamental criterion for the recognition of the various lineages of Pteridophylla in Permo-Carboniferous times, and the understanding of the mode of frond architecture allows to relate the laminar modifications with the general climatic evolution in the corresponding areas during that period.