

The qualitative approach for Carboniferous plant taxonomic analyses: implications of the *Linopteris-Reticulopteris* distinction

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Abstract

Linopteris PRESL, and *Reticulopteris* GOTHAN are the two most common forms of Carboniferous neuropteroid foliage exhibiting reticulate venation. Based on a century of work in Western Europe on the Neuropterids, it can be established that *Linopteris* and *Reticulopteris* show conspicuous differences in their frond architecture. Such differences demonstrate that these genera correspond to taxonomically very different groups of plants. However, *Linopteris* and *Reticulopteris* are still confused in some papers. With the hope of helping everyone to reach the best taxonomic decisions possible, the distinctive characters of *Linopteris* and *Reticulopteris* are briefly analyzed and compared, and some more general considerations are presented.

Key-words

Carboniferous, Pteridosperms, Neuropterids, Frond architecture, *Reticulopteris*, *Linopteris*.

Résumé

L'approche qualitative pour l'analyse taxonomique des plantes carbonifères: les implications de la distinction entre *Linopteris* et *Reticulopteris*. - *Linopteris* PRESL et *Reticulopteris* GOTHAN sont les deux formes les plus communes des plantes carbonifères à feuillage neuroptéroïde et à nervation réticulée. Sur la base d'un siècle de recherches en Europe occidentale sur les Neuroptéridées, il a pu être établi que *Linopteris* et *Reticulopteris* présentent des différences marquantes dans l'architecture de leur fronde. De telles différences démontrent que ces genres correspondent à des groupes de plantes très différents au point de vue taxonomique. Néanmoins, *Linopteris* et *Reticulopteris* sont parfois encore confondus dans certains travaux. Dans l'espoir d'aider chacun à atteindre la meilleure discrimination taxonomique possible, les caractères distinctifs de *Linopteris* et *Reticulopteris* sont brièvement analysés et comparés, et quelques considérations plus générales sont présentées.

Mots clés

Carbonifère, Ptéridospermées, Neuroptéridées, Architecture de la fronde, *Reticulopteris*, *Linopteris*.

I. INTRODUCTION

Among Carboniferous neuropteroid foliage (*i.e.* with pinnules showing a cordate base) a first distinction was quickly established to separate forms with reticulate venation from the originally described forms with open venation.

Additionally, with the increasing information, it was rather quickly noticed that significant differences apparently existed in the frond architecture of the most common genera classified within the "Neuropterids". These distinctions were established over a century ago in the palaeobotanical literature, and for more than fifty years now, the distinction between the genera *Linopteris*

PRESL (1838) and *Reticulopteris* GOTHAN (1941), the two main neuropteroid foliage taxa exhibiting reticulate venation, is no longer a matter of debate in Western Europe. Even though CROOKALL (1959, p. 201-202) placed all reticulate-veined neuropteroid foliage in *Linopteris*, he pointed out clearly the distinctive characters between the Imparipinnate and the Paripinnate members of the group. Surprisingly, and namely in North America, it still is not rare to find confusion (as mentioned in TAYLOR, 1981, p. 386; and in TAYLOR & TAYLOR, 1993, p. 595) between these two genera in some publications and handbooks (for instance STEWART, 1983, p. 258, fig. 21.17 D; reproduced again in STEWART & ROTHWELL, 1993, p. 314, fig. 23.19 D).

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Moreover, the confusion at the nomenclatural level (BELL, 1962, p. 45) may sometimes culminate in confusion at the taxonomic level (PHILLIPS & DiMICHELE, 1998, p. 121-123). It is therefore justified to present an up-to-date brief account on this matter, with the hope of helping everyone to reach the best taxonomic decisions possible in order to avoid inaccurate conclusions in biostratigraphy, palaeoecology, and palaeogeography, where palaeobotanical data are used regularly.

II. BRIEF CRITICAL HISTORICAL REVIEW

The taxon *Neuropteris* was originally differentiated (BRONGNIART, 1822) as a section (*i.e.* subgenus) of the genus *Filicites* SCHLOTHEIM (1820) on the basis of pinnule outline and venation. It was formally raised to generic rank by STERNBERG in 1825, with the spelling *Neuropteris*.

In addition to neuropteroid forms with open venation (as described initially for *Neuropteris*), specimens were found with similar outline but with obvious reticulate venation. The generic name *Dictyopteris* GUTBIER (1835) was accordingly introduced to accommodate such a conspicuous difference in the venation pattern. A few years later, the designation *Linopteris* PRESL (in STERNBERG, 1838) was proposed to replace GUTBIER's designation for nomenclatural reasons. Although nomenclaturally justified, PRESL's designation did not gain immediate acceptance.

For more than a century, two generic names were used for the typical Carboniferous neuropteroid foliage: *Neuropteris* for specimens exhibiting open venation, and either *Linopteris* or *Dictyopteris* (for instance ZEILLER, 1888, p. 289 and others; WHITE, 1897, p. 289 and others) for those exhibiting reticulate venation. It was not until the end of the 19th century that PRESL's designation, *Linopteris*, became more generally accepted. However, before the end of the 19th century, accumulating information had made it clear that the most commonly recorded species of these two genera formed two groups on the basis of frond architectural features. Each of the architectural groups included both reticulate and open venation forms.

For instance, ZEILLER (1878, p. 49) clearly mentioned that the terminal pinnule of the ultimate pinnae of *Neuropteris heterophylla* BRONGNIART is larger than the adjacent lateral pinnules, whereas (p. 50) the terminals of *Neuropteris* (presently *Paripteris*) *gigantea* (STERNBERG) are smaller than the laterals. He also noticed the presence of intercalated ultimate pinnae in *N. heterophylla*, and of intercalated pinnules in *N. gigantea*. In 1886-1888, and in 1900 ZEILLER, though maintaining the primacy of venation characteristics for taxonomic determination, insisted again on the importance of the frond features, emphasizing that the reticulate neu-

ropteroid forms paralleled the open venation forms in exhibiting similar differences in their frond architecture. Patently [and with the exception of the absence of intercalated elements in the frond of *Neuropteris* (presently *Neuraethopteris*) *schlehanii* (STUR), because of the lack at that time of significant data], ZEILLER pointed out most of the characteristics that later became the foundation of more formal designations.

From such an accumulation of information, it was possible for GOTHAN to propose in 1913 a classification dividing the whole group into **Imparipinnatae** (**communes** for those lacking intercalated elements, and **intercalatae** for the others), and **Paripinnatae**. Several species that were classified by GOTHAN into the subgroup *Imparipinnatae communes* (*i.e.* devoid of rachial ultimate pinnae) are now known to exhibit such rachial (=intercalated) pinnae. This was, of course, mainly related to the fact that most diagnostic specimens were found after GOTHAN proposed his classification, but this was not true in all cases. As noticed above, ZEILLER had mentioned, and illustrated (1886, pl. 43, fig. 1; pl. 44, fig. 1), the existence of intercalated ultimate pinnae for *N. heterophylla*. Furthermore, such pinnae are visible on the large specimen of *Neuropteris heterophylla* illustrated by BRONGNIART (1831, pl. 71, fig. 1). For some other related species, for instance *Neuropteris* (presently *Laveineopteris*) *tenuifolia* (SCHLOTHEIM), ZEILLER (1888, p. 273) had also noted the presence of such intercalated pinnae, on the basis of a large specimen (mentioned on p. 275) that was not illustrated because it had been recorded from the Saarbrück area. Consequently, *N. heterophylla* and *N. tenuifolia* should have been classified by GOTHAN within the *Imparipinnatae intercalatae*, and not within the *Imparipinnatae communes* (GOTHAN, 1913, p. 199, 202). These points notwithstanding, GOTHAN continued to use of only two generic names for this entire group of plants, even though he was introducing a formal subdivision of the neuropterids and had made note of characters of the *Paripinnatae* that made it a natural and distinct group (GOTHAN, 1913, p. 194).

It was not until 1941 that GOTHAN introduced a generic classification based on the obvious differences in the frond architecture, supported by the information that had progressively accumulated on the reproductive organs (HALLE, 1933). GOTHAN (1941, p. 427) kept the main two-fold division: **Imparipinnatae**, and **Paripinnatae**. Within each architectural group he proposed two generic names, one for the open venation forms and one for reticulate venation forms, respectively *Imparipteris* and *Reticulopteris* for the *Imparipinnatae*, and *Paripteris* and *Dictyopteris* for the *Paripinnatae*. In addition, GOTHAN proposed keeping the names *Neuropteris* and *Linopteris* for the species (or specimens) for which the available characters were insufficient to allow unambiguous assignment to the above defined taxa. In 1953,

GOTHAN applied that two-fold division, but replaced *Dictyopteris* by *Linopteris*, for nomenclatural reasons. In spite of its use during several years (for instance in GOTHAN & REMY, 1957, and in REMY & REMY, 1959), it was shown (POTONIE, 1956) that the name *Imparipteris* could not validly replace *Neuropteris* on nomenclatural grounds. Thus, the designation *Imparipteris* was rather quickly abandoned.

When comparing GOTHAN's 1941 and 1913 classifications, it appears that an interesting aspect was lost in 1941. It is related to the former subdivision of the Impariplinatae into communes and intercalatae, based respectively on the absence or presence of rachial (intercalated) ultimate pinnae on the main "axes" between the insertions of the bipinnate segments. This loss of precision resulted mainly from two causes.

The first cause is clearly, as noted earlier, the confusion concerning the taxa to be classified within these two subgroups. Such confusion concerning the presence or absence of intercalated pinnae persists for some taxa in GOTHAN, 1953. The example of *N. tenuifolia* is significant in this respect. STOCKMANS (1933) mentioned the presence of such intercalated pinnae for *N. tenuifolia*; GOTHAN (1953, p. 38, 39), however, felt it necessary to raise some doubt in this matter, and to emphasize that STOCKMANS had not illustrated any specimen showing that feature. GOTHAN's remark on this point is, in fact, totally inaccurate. STOCKMANS had previously published (1932) a short paper with a very explicit title, and had illustrated a significant specimen indisputably showing intercalated rachial pinnae. However, as for the specimen mentioned previously by ZEILLER, STOCKMANS' specimen originated from the Saar basin, and had already been illustrated, thus there was no reason for it to be reproduced again in a monograph devoted to the Neuropterids from the Belgian coal basins. Nevertheless, the characteristics of that specimen were mentioned again in STOCKMANS' monograph (1933, p. 15), and the 1932 paper was referenced in the bibliography (p. 59). The second cause results from the fact that the characters on which these subdivisions were founded were considered only from a strict morphological, descriptive viewpoint, focused largely on pinnule characteristics and frond fragments. No attempt was made to analyze the architecture of these imparipinnate fronds from a dynamic viewpoint, and therefore no attempt to understand the significance of rachial (intercalated) ultimate pinnae, inserted directly on the primary rachises of some of these taxa. It is clear that maintaining such a static descriptive viewpoint made it impossible to decipher the significance of all the slight variations exhibited by some of these fronds, and such a misunderstanding of course added to the confusion mentioned above. Consequently, in spite of being mentioned in most descriptions, the presence or absence of rachial intercalated ultimate pinnae was not accounted for systematically. As a result, it

was obviously difficult for GOTHAN to retain such an apparently "variable" characteristic as an important taxonomic character, and this is probably why it disappeared from his 1941 classification, unfortunately. This static position may appear still more surprising in light of some rather usual short but accurate comments about frond development in the Paripinnatae involving a more "dynamic" approach focusing on a bifurcating process [for instance ZEILLER, 1900, p. 105-106: "comme si la fronde était formée des ramifications successives et répétées d'un axe garni toujours des mêmes pinnules (fig. 79)"].

Beside the two-fold subdivision of the Neuropterids into Impariplinatae and Paripinnatae, the idea of having perhaps to segregate *Neuraethopteris schlehanii* (STUR) from the other Neuropterids Impariplinatae began to appear following a short remark in WAGNER (1963, p. 18, 20). WAGNER mainly based his comment on the characteristics of the male reproductive organs, without any precise comments concerning the frond architecture. Otherwise, WAGNER kept a two-fold division for the Neuropterids, by following CORSIN (1960) who recognized the Cyclopteridaceae and Rachivistitaceae.

Soon later, LAVEINE (1966, 1967a), rejecting CORSIN's classification, introduced formally a definite three-fold division, with the designations: "Neuraléthospermées", "Neurodontospermées", and "Parispermées". That proposal was founded on the frond architecture and its mode of differentiation, interpreted on a dynamic basis. More recently, with the help of additional information gathered during nearly thirty years of investigations, an updated version of this classification was proposed (LAVEINE, 1997). Three main types of frond architecture were defined (or re-defined, see for instance GOGANOVA *et al.*, 1993; LAVEINE *et al.*, 1993b): the "bifurcate pinnate" type, the "pseudo-pinnate" type, and the "bifurcate semi-pinnate" type.

The "bifurcate pinnate" type characterizes the genera *Neuraethopteris* CREMER, *Alethopteris* STERNBERG, *Lonchopteris* BRONGNIART (that were included in the LAVEINE's "Neuraléthospermées"), and the more recently proposed genus *Cardioneuropteris* GOGANOVA *et al.* (1993). The only significant change compared to LAVEINE's 1967a interpretation concerns one of the characteristics of the frond. It could be established recently (LAVEINE *et al.*, 1993a) that the frond exhibited a main bifurcation, and was not built according to a "strictly pinnate" model, as previously proposed (LAVEINE, 1967a, fig. 2; WNUK & PFEFFERKORN, 1984, fig. 13). From a restricted descriptive viewpoint, it might be considered that this group would correspond in essence to the Impariplinatae communes previously mentioned. The group is characterized by male reproductive organs of *Whittleseya* type, or allied genera, producing *Monoletes*-type pollen grains.

The "pseudo-pinnate" type, characterizing the genera

Paripteris GOTHAN and *Linopteris* PRESL, was recently thoroughly re-investigated (LAVEINE *et al.*, 1993b). As known for many years, the group exhibits very distinctive characters (LAVEINE, 1997). It corresponds fundamentally to the Paripinnatae. The group is characterized by male reproductive organs of *Potoniea* type, producing trilete *Crassispora*-type pollen grains. The "bifurcate semi-pinnate" type (Fig. 1, A1), characterizing principally the genera *Neuropteris* (BRONGNIART) STERNBERG, *Laveineopteris* CLEAL *et al.*, *Macroneuropteris* CLEAL *et al.*, *Reticulopteris* GOTHAN, and *Odontopteris* BRONGNIART, was analyzed from a general viewpoint in LAVEINE, 1997. It was again re-investigated recently, in an expanded analysis (LAVEINE *et al.*, 1998) devoted to the single species *L. rarinervis* (BUNBURY). From a restricted descriptive viewpoint, the bifurcate semi-pinnate type can be considered to correspond in essence to the Imparipinnatae intercalatae. The information concerning the male reproductive organs for the taxa of this last group is very poor, and very doubtful.

Together with the many other available characteristics, these three categories provide a basis to group most of the taxa assigned to the Neuropterids *sensu lato*. As mentioned again recently (LAVEINE *et al.*, 1998, p. 416) this does not mean that some other types of fronds may not exist, but they will have to be reliably "substantiated" by the presentation of significant specimens, allowing a clear interpretation of their whole frond architecture. Such a compulsory requirement is a first essential step for a clear understanding either of their eventual relationship (ancestrality or derivation), or of their total independence.

The designations *Laveineopteris* CLEAL *et al.*, and *Macroneuropteris* CLEAL *et al.* mentioned above bring the opportunity to point out that during the last decade CLEAL *et al.* (1990), and CLEAL & SHUTE (1995) have introduced a re-classification of the Neuropterids on the basis of cuticular information. Some comments on this matter have already been presented in recent papers (LAVEINE, 1997, p. 176-182; LAVEINE *et al.*, 1998, p. 422-426). Here is not the place to introduce additional

comments, except that the proposed classification concerns essentially the generic level, stressing the cuticular differences between these genera. As a recent example in this respect, and because it may be considered peripherally related to the matter of the present paper, the genus *Barthelopteris* was recently proposed (ZODROW & CLEAL, 1993) for removing from *Reticulopteris* the species *R. germarii* (GIEBEL) from its assignment to *Reticulopteris*, on the sole basis of cuticular differences. Because some points remain to be elucidated for the Stephanian species of *Reticulopteris* concerning the variability of both the general morphological characteristics of the foliage and of the cuticular characteristics, the following comparison between *Linopteris* and *Reticulopteris* will be mainly restricted for *Reticulopteris* to the characteristics of the type species, *R. muensteri* (EICHWALD).

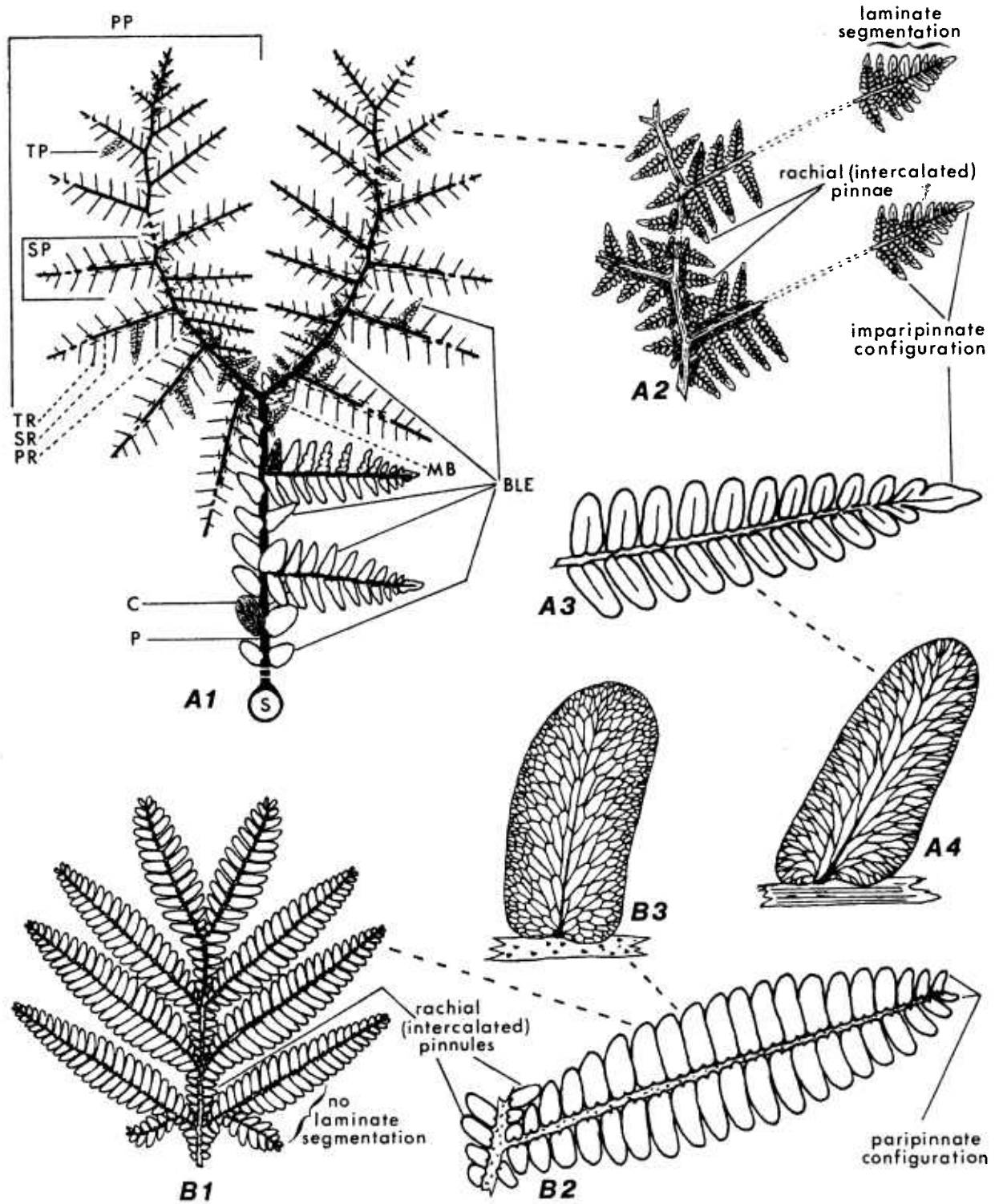
III. *LINOPTERIS* AND *RETICULOPTERIS*, COMPARED AND CONTRASTED

III.1. External morphological features

The morphological characteristics of the foliage of these two genera being well known and nicely circumscribed, the following comparison will be kept as succinct as possible.

As mentioned above, the fronds of *Linopteris* are of the pseudo-pinnate type (LAVEINE *et al.*, 1993b, text-fig. 11; LAVEINE, 1997, fig. 3), whereas those of *Reticulopteris* appear similar to those of *Neuropteris*, which are of the bifurcate semi-pinnate type (LAVEINE, 1997, fig. 13, or fig. 19, right hand side). In spite of the fact that a specimen showing the main bifurcation has not yet been produced for *Reticulopteris muensteri*, all the other available characteristics leave no doubt about the bifurcate semi-pinnate architecture (Fig. 1, A1) of the fronds of *Reticulopteris*. The distinction between these two genera is equally clear even at the level of the rather small-sized remains that are usually reported in the literature. These characteristics will be briefly, and critically compared.

Fig. 1: A.- *Reticulopteris muensteri* (EICHWALD). A1, General synthetic drawing illustrating the main characteristics that may be exhibited by the "bifurcate semi-pinnate" frond of *Reticulopteris*. For the sake of distinctness, the various elements are not strictly to scale, the dotted lines indicating that the corresponding parts could reach greater dimensions. P = petiole; MB = main bifurcation; PR, SR, TR = primary, secondary, tertiary rachises; PP, SP, TP = primary, secondary, tertiary pinnae; C = *Cyclopteris* (or cyclopteroid elements); BLE = basic laminate elements; S = stem (thick black lines corresponding to the "fundamental rachis" and its bifurcations, thin lines to the "basic laminate elements"); A2, more detailed schematic drawing of the near terminal part of a primary pinna; A3, general outline of an ultimate pinna showing its single large terminal pinnule (imparipinnate configuration), and the distal lateral pinnules still partly attached to the supporting rachis; A4, venation diagram of a fully developed pinnule. B.- *Linopteris* sp. B1, schematic drawing of part of the pseudo-pinnate frond, with simple entire pinnules present on all the rachises; B2, ultimate pinna with a general ovate outline, attached to the supporting rachis, and with two small terminal pinnules (paripinnate configuration), all the rachises bear randomly distributed stout emergences; B3, venation diagram of a fully developed pinnule.



III.1.1. Ultimate pinnae

Although the type specimen (figure reproduced in CROOKALL, 1959, p. 203, text-fig. 68) of *R. muensteri* is fragmentary, and devoid of its terminal part, it was shown in early studies (see for instance ZEILLER, 1886, pl. 49, fig. 2) that the ultimate pinnae are imparipinnate. As a result, the main vein of the single terminal pinnule is the prolongation of the rachis of the ultimate pinna (Fig. I, A3; Pl. I, fig. 2a, 2b; Pl. III, fig. 7a). The terminal pinnule, although sometimes slender and of small size (Pl. III, fig. 1), is nevertheless always larger than the nearby lateral pinnules (see for instance BELL, 1962, pl. 38, fig. 1). The existence for these fronds of a laminate segmentation (LAVEINE, 1997, fig. 17; Fig. I, A2; Pl. II, fig. 5), which can reach at most a slightly bipinnatifid stage (see for instance BELL, 1962, pl. 38, fig. 2), involves some important morphological characteristics. A first important characteristic is that the lateral pinnules of an ultimate pinna result clearly from the successive differentiation of lateral lobes more or less alternately produced from the apex. Consequently the terminal pinnule shows often a rhombic outline usually with one lateral lobe expressed (Pl. I, fig. 2b; Pl. III, fig. 7a), and sometimes two (Pl. III, fig. 6, 6a). In areas proximate to the terminus of the ultimate pinna, the nearby lateral pinnules often are fully or still partly attached to the rachis of the ultimate pinna (Pl. III, fig. 2a, 7a). It is only when moving basipetally (Pl. I, fig. 2a; Pl. II, fig. 2a; Pl. III, fig. 2, 3) that the lateral pinnules become progressively differentiated, manifesting a typical "neuropteroid" outline. It is, therefore, appropriate to analyze the differentiation in moving down from top to base. However, it is worth emphasizing here that one must always keep a certain "flexibility" in the analysis: it is advantageous with compound foliage to practice an "upward" as well as a "downward" look. Because the first differentiated lateral pinnules are the basal ones, it is also justified, and useful, to consider the differentiation from base to top, according to the chronology of formation: the lobe of the terminal in that case is consequently a lateral pinnule that has not reached its full stage of differentiation, and this remark holds also more or less for the still partly attached nearby laterals, explaining their rather large coherence to the rachis. Such a rather strong coherence of the lamina near the apex explains why the terminal parts of ultimate pinnae are the most resistant to disaggregation. *The taphonomical consequence is that these parts are the most easily preserved, and consequently the most commonly recorded.* When an imparipinnate neuropteroid form is present at a site, it usually takes only a short time to record such imparipinnate fragments, which exhibit clearly their terminal imparipinnate configuration. Another important characteristic resulting from the laminate segmentation (Fig. I, A2) in these bifurcate semi-pinnate fronds is that the terminations of all the ramifi-

cations of the "fundamental" rachis (LAVEINE *et al.*, 1998, p. 383) exhibit all the transitional stages (*i.e.* lobate pinnules) between simple pinnules and ultimate pinnae (see for instance LAVEINE *et al.*, 1993b, fig. 1B; or here Pl. I, fig. I; Pl. II, fig. 3, 5). As a result, it is usually possible, although less common, to find some lobate pinnules among the remains recorded at a site (for instance ZEILLER, 1886, pl. 49, fig. 5; or LAVEINE, 1967a, pl. 60, fig. I).

Conversely, the pseudo-pinnate fronds of *Linopteris* are characterized by a total lack of laminate segmentation (LAVEINE *et al.*, 1993b; LAVEINE, 1997, fig. 3). The highly compound frond results strictly from repeated rachial bifurcations of a fundamental rachis bearing simple, entire pinnules (Fig. I, BI). The "ultimate pinnae" exhibit a paripinnate configuration (LAVEINE *et al.*, 1993b, fig. 3-4); the two "terminal" pinnules (in fact the "last laterals") are smaller than the adjacent ones (Fig. I, B2). All the pinnules are distinct laminar entities developed from separate lamina primordia (see for instance BOWER, 1923, fig. 87). As a result all the pinnules, even the terminals, are attached to the rachis only by a small punctiform area, from where they were apparently easily abscised. As a consequence of these fundamental characteristics, it is rather rare to find intact pieces of foliage of *Linopteris*. The most common specimens are slabs with huge amounts of dispersed pinnules, never lobate, exhibiting clearly the restricted point of previous insertion to the rachis (see for instance LAVEINE *et al.*, 1993b, pl. 3, fig. 1, and 4-6).

III.1.2. Pinnule outline and variability

Normally developed pinnules, *i.e.* those located in the middle part of the pinnae (*cf.* footnote of SCHIMPER, 1869, cited in LAVEINE, 1997, p. 157) are elongate ovate in outline, with a cordate base. Consequently, pinnules of *Reticulopteris* such as those of the specimen illustrated in LAVEINE (1967a, pl. 58, fig. 3), if found isolated (Pl. 3, fig. 3a), might bear a certain resemblance to some pinnules of *Linopteris* (for instance LAVEINE, 1967a, pl. 79, fig. 5). This may explain some of the confusion previously mentioned. However, such confusion is possible only when sample sizes are small. Otherwise, it seems rather easy to make the distinction (Pl. III, fig. 4a), at least in Western Europe and in North America. The range of pinnule size variation also differs between *Linopteris* and *Reticulopteris*, even where the average size of the pinnules varies greatly from one level to another, probably as a response to palaeoecological variations. Apart from the variation in the general outline from roundish to elongate sickle-shaped pinnules (as illustrated for *Paripteris* in LAVEINE *et al.*, 1993b, pl. 1, fig. 1), the pinnules of *Linopteris* recorded from a given level are characterized by a rather narrow range of size

variation. This is not at all the case for *Reticulopteris* (GOTHAN, 1953, pl. 33), for which it is well known that the size of the pinnules from a single site may vary greatly, from small pinnules 5 mm long (Pl. III, fig. 1, 1a) to large pinnules of the “*impar*” type (Pl. II, fig. 6; Pl. III, fig. 6, 6a), that may be up to 8 cm long. Accordingly, the size of the terminals corresponding to these various kinds of “ultimate” pinnae may also greatly vary (Pl. III, fig. 1, 6).

III.1.3. Venation

Although the venation is reticulate for both genera, it has been mentioned for more than a century that the reticulation is more regularly organized (Fig. 1, B3) in *Linopteris*. For *Reticulopteris*, the lateral veins are more loosely anastomosed, with all possible transitions between pseudoanastomoses and perfect anastomoses (Fig. 1, A4; Pl. II, fig. 2a; Pl. III, fig. 2a, 4a, 5a, 7a). An excellent recapitulation on this matter was provided recently (ZODROW & CLEAL, 1993), and applies with no difficulty for the specimens reported from Western Europe and North America. To our knowledge, there is only one case of *Linopteris* reported from Western countries (including North Africa) for which the venation may exhibit a somewhat flexuous appearance: it concerns *L. regniezii* (LAVEINE, b; 1967a, b; presently *Linopteris bronngniartii* fa *regniezii*, according to ZHANG *et al.*, 1993). It is because of its flexuous venation that this form was previously confused with *R. muensteri* (JONGMANS, 1952), but the general outline of the dispersed pinnules, their rather constant size, and the presence of typical “orbicular” pinnules leave no doubt concerning their attribution to *Linopteris*.

In Western countries, there seem to be no transitional forms between the reticulate venation of *Linopteris* and the open venation of its probable ancestor *Paripteris*. This contrasts strongly with *Reticulopteris*, for which the similarities with either *N. heterophylla* and/or *N. obliqua* (BRONGNIART) were pointed out for nearly a century. It was shown (JOSTEN, 1962) that a whole transitional series existed between *N. obliqua* and *R. muensteri* concerning the expression of the reticulate venation. It is worth emphasizing that it is rather common to find all transitions between pseudo-anastomosing and true anastomosing venation, even at a single fossiliferous site rich in *Reticulopteris* remains (Pl. II, fig. 3, 3a, and Pl. III, fig. 2, 2a for instance).

III.1.4. *Cyclopteris* (or cyclopteroid elements)

The bifurcate semi-pinnate frond usually bears in its proximal parts (Fig. 1, A1) large roundish folioles with a radiating venation, known as *Cyclopteris* (or cyclopteroid elements). They have been known in

Reticulopteris for a long time (for instance ZEILLER, 1886, pl. 49, fig. 4, reproduced in LAVEINE, 1967, pl. O, fig. 3). They exhibit a more or less similar reticulate pattern, which is, however, sometimes difficult to observe, with fewer meshes as compared to the normal pinnules. This is particularly true near the margin, where the veins exhibit a more parallel course. An excellent illustration of this point is provided in REMY & REMY (1977, fig. 143 b). For *Linopteris*, it is well known that the “orbicular” pinnules in the angles of the bifurcations, because of space constraints, show a roundish outline that might be compared with the outline of *Cyclopteris*, but these pinnules are always of smaller size in Western countries. It was speculated by LAVEINE (1967a, fig. 7) that perhaps in the very basal part of the frond such pinnules may have reached a larger size, comparable to some of the smaller *Cyclopteris* of the bifurcate semi-pinnate fronds, but this will probably remain purely speculative. The ease with which *Linopteris* pinnules abscise makes it highly unlikely that a specimen will be found with attached basal cyclopteroid elements, particularly since first-formed basal pinnules of the frond would be the most likely to abscise first.

III.1.5. Intercalated (rachial) elements

For *Linopteris*, it was definitely established from the beginning (GUTBIER, 1836, pl. 11, fig. 7) that all the rachises bear simple, entire pinnules (see LAVEINE *et al.*, 1993b, for a recapitulation on this point).

For *Reticulopteris*, although the presence of intercalated ultimate pinnae (Fig. 1, A2) is usually mentioned in the general descriptions (for instance REMY & REMY, 1977, p. 261), there is to our knowledge a lack of pertinent illustration on this point, to the exception of an illustration provided by BOERSMA (1981, fig. 4), of a specimen recorded from the roof of the “Flöz Zweibänke”, at Piesberg (personal information kindly provided by Drs. H.W.J. VAN AMEROM and J. VAN DEN BURGH): the specimen shows the imparipinnate configuration and some intercalated pinnae on a primary rachis, but not the venation because of the reduced magnification. Apparently, it was mainly on the basis of the similarity of the frond construction with *Neuropteris* that this characteristic was usually asserted. It is therefore relevant to illustrate here some additional specimens from the Northern France coal field, demonstrating clearly that the *Reticulopteris* frond is actually built according to the bifurcate semi-pinnate type (Pl. I; Pl. II, fig. 1, 1a, 3, 4).

III.1.6. Rachises

It again has been known for a long time that the rachises of the genera *Paripteris* and *Linopteris* (=Parispermaceae) are not only longitudinally striated, but also

usually bear randomly distributed stout emergences (LAVEINE *et al.*, 1993b, pl. 7, fig. 4 for instance). Although the density of these emergences may vary within great limits (LAVEINE *et al.*, 1993b, p. 88), such conspicuous emergences are, among the taxa usually assigned to the Neuropterids, only reported for these two genera. Conversely, the rachises of *Reticulopteris* are only markedly striated longitudinally (Pl. I, fig. 2a, 2c; Pl. II, fig. 1a, 2).

It may be of some interest to add a short comment on the information provided by some of the specimens presented here. The primary rachis of the *Reticulopteris* specimen illustrated Pl. I, fig. 1, 1a is 7 mm wide, and the complete secondary pinna attached on the right side is 29 cm long. Account taken of the angles of insertion, the total width of the primary pinna at that level is therefore approximately 50 cm, and the width of the frond is about 1 m. From the dimensions of the rachises of the specimen presented Pl. II, fig. 1, 1a, 2, the width of the primary rachis can be estimated at 28 mm, and 12 mm for the secondary rachises inserted sub-oppositely (Pl. II, fig. 1). Despite the fact that experience has shown that no direct proportionality can be inferred in such cases, one can nevertheless easily guess that some fronds of *Reticulopteris* could be of rather great size. In the case of the latter specimen, a minimum width of 1.2 m is a reasonable estimation for the primary pinna, and consequently it involves a 2.4 m minimum width for the whole frond.

III.2. Anatomical features

As summarized in LAVEINE *et al.* (1993b, p. 100-101), the relationship between some permineralized stems (and frond members) of the *Sutcliffia* type with compression foliage of the *Linopteris* type can be now considered as definitively established, based on the work of PHILLIPS & ANDREWS (1963) and STIDD *et al.* (1975). PHILLIPS & ANDREWS clearly demonstrated the connection between the stem *Sutcliffia insignis* SCOTT and attached petioles bearing external massive emergences 1 to 1.5 mm long (PHILLIPS & ANDREWS, 1963, pl. I, fig. 2-3, pl. 5, fig. 14), involving the creation of a variety *tuberculata*.

STIDD *et al.* provide additional important information; in addition to the presence of massive emergences on the rachises, it is shown that there are vascular traces passing to the adaxial surface of other than ultimate rachises. This anatomy suggests the presence of rachial pinnules on the rachises of various orders. Such rachises exhibiting the combination of both stout emergences and rachial pinnules are, for compression remains, known only within the Parispermaceae. Furthermore, the numerous associated pinnules present in the coal balls studied by STIDD *et al.* are clearly, from the aspect of their reticulate venation (STIDD *et al.*, 1975, plate 2, fig.

5, 10), of the *Linopteris* type. It can be added that the nearly complete pinnule illustrated pl. 2, fig. 10 is very likely an "orbicular" pinnule, which shows clearly its point of attachment.

From all these facts, and from the strict correlation between the information derived from both permineralized and compressions remains, it can be concluded that the relationship between the compression foliage *Linopteris*, and the stem *Sutcliffia*, proposed by STIDD *et al.* (1975), is beyond any contest. In their search for the eventual possible compression taxa that may present some features correlatable with their permineralized remains, STIDD *et al.* felt it necessary, however, to look beyond *Linopteris sensu stricto* at specimens of *Linopteris (Reticulopteris) muensteri* and *L. rubella* LESQUEREUX (a later synonym of *R. muensteri*); it is rather funny that they deplored the lack of significant specimens for these species. As shown for instance by the specimen illustrated by BELL (1962, pl. 38, fig. 2) there are no intercalated pinnules in the normally developed bifurcate semi-pinnate fronds. The only place in the frond where a few intercalated pinnules might have existed (and corresponding in fact to non-differentiated intercalated pinnae) would be near the terminal part of the primary pinnae, when development of the primary pinnae was ending through a regular decrease (LAVEINE, 1997, fig. 13 A). There are of course intercalated (rachial) "pinnules" in the bifurcate semi-pinnate fronds of the genus *Macroneuropteris* CLEAL *et al.*, but these "pinnules" are in fact homologous of the "basic laminate elements" of the normally developed frond of *Neuropteris* (LAVEINE, 1997, fig. 15).

III.3. Reproductive features

On the basis of almost constant association, it is now almost unanimously agreed that the male reproductive organs of *Potoniea* ZEILLER type are the male reproductive organs of the Parispermaceae. These organs are organized in specialized male apparatuses (LAVEINE *et al.*, 1993b) not directly related with the foliage. Consequently, there is almost no hope (except for the discovery of a whole tree perfectly preserved in all its parts!) of improving the relationship beyond the argument of constant association between *Potoniea* type male organs and remains of foliage either of *Paripteris* or *Linopteris*.

Although the genus *Psaliangium* was created by REMY (1953) to accommodate some poor fertile remains associated with some reticulopteroid foliage from the Stephanian, that attribution is in need of more significant data, and must be considered for the time being as very doubtful. Even REMY & REMY (1977, p. 124) did not mention it, whereas they described *Potoniea* among the microsporangiata taxa of the pteridosperms.

III.4. Some remarks concerning the preceding comparative account

According to the arguments developed above, it seems rather easy to distinguish *Reticulopteris* from *Linopteris* on the basis of the morphological characteristics of typical compression specimens. However, it was sometimes necessary to qualify this characterization by noting that it applied only to specimens of Western countries. Thus, this remark calls for some additional comments. The morphological variability of *Linopteris* and its ancestor *Paripteris* is rather restricted in Western countries, but not in specimens from Eastern Asia. Whereas in Western countries, the size of the pinnules of *Linopteris* may vary from 7 mm to approximately 4 cm at most (but, as mentioned previously, with a restricted range of variation at any given level), in North China some pinnules may reach a 7-8 cm length, and can be found together with smaller ones (ZHANG *et al.*, 1993, pl. 26, fig. 1). Consequently, such large pinnules may be as large as some pinnules of the *impar* type of *Reticulopteris*. Moreover, the outline of the pinnules in Western countries may vary from straight to sickle-shaped with an obtuse rounded apex. In North China the variability on this point is also far greater. Together with straight to sickle-shaped pinnules with a rounded apex, there may be large pinnules of more triangular outline with an acute apex (ZHANG *et al.*, 1993, pl. 27, fig. 10; LAVEINE *et al.*, 1993b, pl. 3, fig. 14-15). Furthermore, the reticulate venation of the pinnules of *Linopteris* in Western countries is usually characterized by a faintly marked midrib and by regularly organized meshes (Fig. 1, B3). In North China, some pinnules may exhibit a well marked midvein, extending up to the apex (ZHANG *et al.*, 1993, pl. 27, fig. 10, 14), and the reticulation may appear somewhat flexuous (ZHANG *et al.*, 1993, pl. 26, fig. 1-2), although it consists nevertheless of true anastomoses. Consequently, in North China, when taking into account only a few pinnules of *Linopteris*, and especially those of triangular outline with a well marked midrib, there might eventually be some possibility of confusion (LI *et al.*, 1992, pl. 4, fig. 7-8) with *Reticulopteris*. It is worth stressing here that there is, however, no doubt concerning the attribution of such pinnules to *Linopteris*. As mentioned previously (ZHANG *et al.*, 1993, p. 30), specimens exist in the private collection of the late Mr. WANG in Lanzhou, ascertaining this attribution. One of the present authors (J.-P. L.) has in his reference collection some colour slides (ref. CHI 94-791 to 794) of a plate prepared by Mr. WANG for a project of publication (which probably will never be published, unfortunately), which show a remarkable paripinnate apex of such a *Linopteris*. The authorization to make the slides was obtained from the Gansu Bureau of Geology and Mineral Resources under the promise not to reproduce elsewhere the photo of the specimen; consequently it can not be illustrated here.

To conclude on this point, it is necessary to be very careful when dealing with linopterids from North China because usually of the great polymorphism of the Parispermaceae at a given stratigraphic level (which, of course, makes the taxonomic treatment rather difficult, see ZHANG *et al.*, 1993, p. 23-33). However, and even if taxonomic determination for the Chinese material appears more arduous than for collections from Western countries, it is nevertheless possible to make one's decision on the basis of the morphological characteristics discussed above.

IV. APPLICATION TO SOME NORTH AMERICAN DETERMINATIONS. IMPLICATIONS

As mentioned above, if it is possible to determine the taxonomic affinities of specimens from North China where the range of morphological variation is high, one could assume that determinations could be reached easily in North America, where the range of variation is much less, comparable to that of Western Europe.

Given that the differences between the two genera are extensive and conspicuous and go well beyond patterns of venation, it is noteworthy that confusion still exists. Consider the summary in TAYLOR & TAYLOR (1993, p. 595): "Some authorities believe that *Linopteris* and *Reticulopteris* may be distinguished by the pseudoreticulate venation in the latter, in which the veins bend toward one another but do not actually anastomose. Others have suggested that the two taxa merely represent variations of a single genus. At least one *Linopteris* species is thought to have been produced by the medullosan seed fern *Sutcliffia*." The extensive differences between these two taxa in many morphological features, including frond architecture make it difficult to defend the position that they are merely variations of a single genus. Furthermore, some specimens of *Reticulopteris* may exhibit true anastomoses (Pl. III, fig. 4a, 5a). Consequently generic determination can not rely solely on venation. Although venation is often a good preliminary indicator, further steps are needed, such as identification of imparipinnate terminations, or lobate pinnules. Two examples of different bearing will be briefly analyzed here concerning the *Linopteris-Reticulopteris* distinction.

IV.1. The STEWART, 1983 specimen

Illustrated in STEWART (1983, p. 258, fig. 21.17 D), and reproduced again in STEWART & ROTHWELL (1993, p. 314, fig. 23.19 D), the specimen shows only part of an ultimate pinna. From the flexuose venation, with a mixture of apparently true and pseudo-anastomoses, this specimen is very likely a *Reticulopteris*.

Although it may be the result of the overlapping of the pinnules, the general outline of the pinnule also favors attribution to *Reticulopteris*. This determination would not be worthy of discussion were it not for the excellence and success of the text book in which it is included. Because of book's great audience, future editions should either change the illustration or the corresponding determination, unless the terminal part of the pinna is preserved (which is impossible to decide from the illustration) and exhibits an indisputable paripinnate termination. In that case, it would be the present authors who would have to strongly revise their pretence concerning the possibility of distinguishing these two taxa on such restricted available information!

IV.2. The PHILLIPS and DiMICHELE, 1998 *Sutcliffia* - *Reticulopteris* relationship

In a recent paper, PHILLIPS & DiMICHELE (1998, p. 119-120) have correlated *Sutcliffia* with *Reticulopteris* type of foliage, and correlatively (p. 123) have raised some doubt about the *Sutcliffia* - *Linopteris* relationship proposed by STIDD *et al.* (1975). Although the remarks of PHILLIPS & DiMICHELE are somewhat made "en passant", their bearing is so important, and the eventual possibly derived consequences so numerous that it was the impulse for the present authors to exchange some comments on this point, and to finally decide to prepare the present common contribution. Because the implications are diverse, it is necessary to organize the discussion step by step.

EXPLANATION OF PLATES

Except otherwise stated, specimens are figured natural size. Some are stored in the collections of the Laboratory of Palaeobotany of the University of Lille I (registration numbers: HBNPC 647419 to 647425), the others are from the BELHIS collection of the Lille Coal Museum (registration numbers: MBL 18 607, 18715, 18716, 19246, 19249, 19253, 19254).

Plate I

Reticulopteris muensteri (EICHWALD)

Fig. 1: Part of a primary pinna showing clearly the characteristic dichotomous-anisotomous mode of branching of the bifurcate semi-pinnate type of frond, note on the right side the presence of a nearly complete "secondary" pinna, and on the left side some fragmentary ultimate pinnae belonging to the more proximal bipinnate lateral segment (more completely preserved on the non-illustrated counterpart, registered as MBL 18248); 1a.- Part of the primary rachis, with most of the rachial (intercalated) pinnae preserved (arrows) between the two successive bifurcations; 1b.- Several ultimate pinnae at the upper side of the nearly complete right lateral ramification, showing their imparipinnate configuration; 1c.- The uppermost right part of the specimen, showing the striate rachis, and the outline and venation of a few pinnules.

Origin: Northern France coal field, Bruay, Pit 6, seam 22.

Stratigraphic interval: Assise de Bruay, upper part of Faisceau de Six Sillons; middle Westphalian C.

Accession number: MBL 19253.

Fig. 2: Part of a primary pinna also showing the dichotomous-anisotomous mode of branching of the bifurcate semi-pinnate type of frond; 2a.- View of the primary rachis, with the proximal part of the right lateral ramification showing two ultimate imparipinnate pinnae nicely preserved; 2b.- Ending of the right ultimate pinna of fig. 2a, showing its imparipinnate configuration; 2c.- The upper part of fig. 2a, showing the longitudinally striate rachis, and some attached rachial (intercalated) pinnae. The right intercalated pinna is slightly bipinnatifid, showing the proximal part of a small pinna on its acroscopic side. A few pinnules show their conspicuous reticulate venation.

Origin: Northern France coal field, Fouquières les Lens, Pit 6 South, seam Edmond supérieur.

Stratigraphic interval: Assise de Bruay, middle part of Faisceau d'Ernestine; upper Westphalian C.

Accession number: MBL 18716.



IV.2.1. The PHILLIPS and ANDREWS, 1963 relationship between the *Sutcliffia* stem structure and the presence of strong emergences (= var. *tuberculata*) on the petiole

This relationship is indisputable, as the petiole was found to be organically connected to the stem.

According to the morphological information derived from compressions, the search for a connection among the Medullosales *sensu lato* has to be restricted to the genera *Paripteris* and *Linopteris*, the only ones to exhibit strongly punctate rachises. Owing to the stratigraphic level of the coal ball studied [Herrin (No. 6) Coal, Carbondale Formation], and owing to the recognized vertical range of *Paripteris* in the U.S.A., which ends at

the top of the Kanawha Formation (LYONS *et al.*, 1985), there remains only *Linopteris* as the possible related foliage.

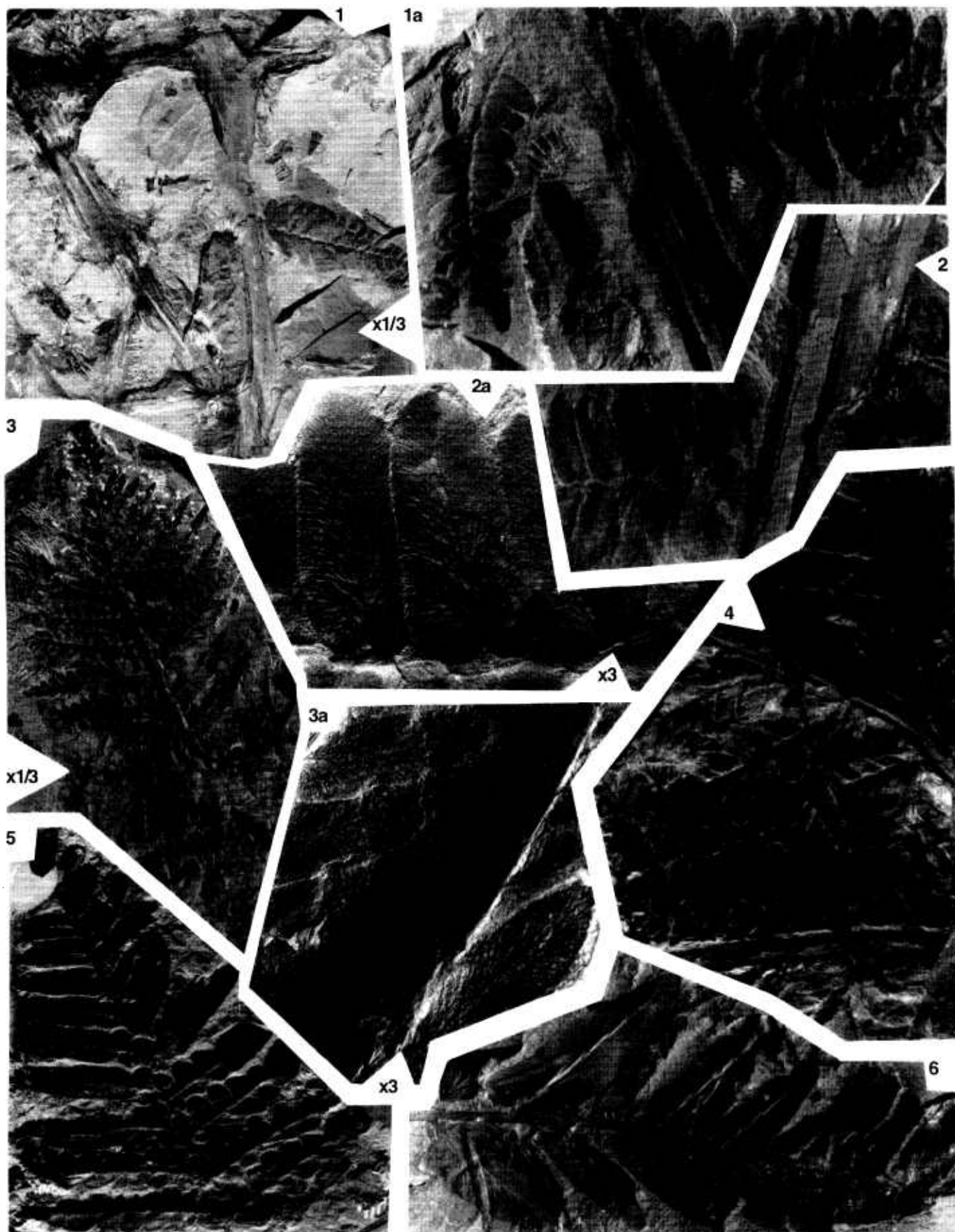
IV.2.2. The STIDD *et al.*, 1975 additional information

There seems to be no doubt concerning the attribution of the studied permineralized remains to *Sutcliffia insignis*, var. *tuberculata*. As an addition to the previous information, it is worth mentioning the presence of vascular traces probably to rachial pinnules. As noticed previously, such rachial pinnules are present on all rachises in the genera *Paripteris* and *Linopteris*. Owing again to the stratigraphic levels from which the coal-balls were secured, it restricts again the possible connection to

Plate II

Reticulopteris muensteri (EICHWALD)

- Fig. 1: Part of a primary rachis of rather large size, probably located in the middle part of a large primary pinna, and showing two successive sub-opposite departures of secondary rachises. Two rachial (=intercalated) pinnae are still attached to the primary rachis; 1a.- View of the middle part of the specimen, and of the rachial pinnae (the base of the left rachial pinna and its attachment to the primary rachis is missing on this part).
- Fig. 2: Counterpart of the specimen on fig. 1, showing on its right side the base of the left rachial pinna of fig. 1a, and its actual attachment to the large primary rachis, longitudinally striated; 2a.-Enlargement of two pinnules at the left side of fig. 2, showing the reticulate venation.
Origin: Northern France coal field, Slag heap of ancient pit of Noyelles-Godault (Dourges n° 4).
Stratigraphic interval: Very likely assise de Bruay, either Faisceau de Six Sillons or Faisceau d'Ernestine; Westphalian C.
Accession number: respectively HBNPC 647419 and 647420.
- Fig. 3: Apical portion of a primary pinna, probably ending at a dichotomy (the base of the right ramification, apparently of equal importance, is only visible for a short distance); 3a.- Enlargement of part of an ultimate pinna from the upper right-hand side of fig. 3, showing the outline of the pinnules and their venation.
Origin: Northern France coal field, Bruay, Pit 6, seam 22.
Stratigraphic interval: Assise de Bruay, upper part of Faisceau de Six Sillons; middle Westphalian C.
Accession number: MBL 19254.
- Fig. 4: Partial view of a specimen showing a near apical portion of a primary pinna, probably ending at a dichotomy.
Origin: Northern France coal field, Hénin-Liétard, Pit 4 South, level between the seams Albraque and St Jacques.
Stratigraphic interval: Assise de Bruay, upper part of Faisceau de Six Sillons; middle Westphalian C.
Accession number: HBNPC 647422.
- Fig. 5: Near apical portion of a secondary pinna, showing all the transitions between simple entire lateral pinnules and ultimate pinnae (laminar segmentation).
Origin: Northern France coal field, Fouquières les Lens, Pit 6 South, seam Edmond supérieur.
Stratigraphic interval: Assise de Bruay, middle part of Faisceau d'Ernestine; upper Westphalian C.
Accession number: MBL 18715.
- Fig. 6: Part of a pinna of the *impar* type, probably located in the proximal part of the frond (a large "pinnule" of *impar* type is homologous to a normally developed ultimate pinna in the distal part of the frond).
Origin: Northern France coal field, Lens, Pit 4, seam B.
Stratigraphic interval: Assise de Bruay, middle part of Faisceau de Six Sillons; lower Westphalian C.
Accession number: MBL 18607.



Linopteris. Furthermore, abundant pinnules of outline and venation typical for *Linopteris* are associated in the coal-balls. All these arguments converge to an indisputable relationship between the specimens of *Sutcliffia insignis* var. *tuberculata* described by STIDD *et al.* with the foliage *Linopteris*. This point seems actually to be beyond any contest.

IV.2.3. The extension of the relationship to *Paripteris* by LAVEINE *et al.* (1993b)

LAVEINE *et al.* hypothesized that the genus *Paripteris* might also possess a *Sutcliffia* type of stem, on the basis of great confidence in the anatomical studies mentioned above, and strong morphological similarities among all

Plate III

Reticulopteris muensteri (EICHWALD)

- Fig. 1: Fragmentary ultimate pinnae, with slender pinnules; 1a.- Enlargement of the right part of fig. 1, showing the venation with a mixture of pseudo and true anastomoses.
Origin: Northern France coal field, Anzin, Pit Cuvinot, slag heap
Stratigraphic interval: Very likely assise de Bruay, either Faisceau de Six Sillons or lower part of Faisceau d'Ernestine; Westphalian C.
Accession number: HBNPC 647425.
- Fig. 2: Fragmentary ultimate imparipinnate pinnae; 2a.- Enlargement of the near terminal part of the pinna at right side of fig. 2, showing the distal lateral pinnules still partly attached by their base to the rachis, and their conspicuous reticulate venation.
Origin: Northern France coal field, Bruay, Pit 6, seam 22.
Stratigraphic interval: Assise de Bruay, upper part of Faisceau de Six Sillons; middle Westphalian C.
Accession number: MBL I9246.
- Fig. 3: Fragmentary ultimate imparipinnate pinnae, and detached pinnules; 3a.- Enlargement of one of the detached pinnules, showing its finely anastomosed venation.
Origin: Northern France coal field, Hénin-Liétard, Méricourt, Pit 3 West, seam Alfred.
Stratigraphic interval: Assise de Bruay, lower part of Faisceau d'Ernestine; middle Westphalian C.
Accession number: HBNPC 647423.
- Fig. 4: Small specimen showing a detached pinnule, and the terminal ending of an imparipinnate pinna; 4a.- Enlargement showing the nicely preserved venation, exhibiting true anastomoses.
Origin: Northern France coal field, Slag heap of ancient pit of Noyelles-Godault (Dourges n° 4).
Stratigraphic interval: Very likely assise de Bruay, either Faisceau de Six Sillons or Faisceau d'Ernestine; Westphalian C.
Accession number: HBNPC 647421.
- Fig. 5: Fragmentary ultimate pinnae, with pinnules of various size, at the verso of the slab illustrated on fig. 3; 5a.- Enlargement of the upper right part of the specimen. The venation of the terminal pinnule, probably of the *impar* type, at the right side of the illustration, is nicely preserved.
Origin: Northern France coal field, Hénin-Liétard, Méricourt, Pit 3 West, seam Alfred.
Stratigraphic interval: Assise de Bruay, lower part of Faisceau d'Ernestine; middle Westphalian C.
Accession number: HBNPC 647423.
- Fig. 6: Fragments of foliage of the *impar* type, most of the pinnules bear several coiled tubes of *Spirorbis*; 6a.- Enlargement of the large terminal pinnule with two sub-opposite lateral lobes.
- Fig. 7: Fragmentary ultimate pinna, at the verso of the slab illustrated on fig. 6; 7a.-Enlargement showing the conspicuous reticulate venation, and again several coiled tubes of *Spirorbis*.
Origin: Northern France coal field, Slag heap of ancient pit of Noyelles-Godault (Dourges n° 4).
Stratigraphic interval: Very likely assise de Bruay, either Faisceau de Six Sillons or Faisceau d'Ernestine; Westphalian C.
Accession number: HBNPC 647424.
- Fig. 8: Partial view of a rather large bipinnate fragment, covered with numerous coiled tubes of *Spirorbis*.
Origin: Northern France coal field, Bruay, Pit 6, seam 22.
Stratigraphic interval: Assise de Bruay, upper part of Faisceau de Six Sillons; middle Westphalian C.



members of the Parispermaceae (including the reproductive organs, and the pollen grains). They therefore postulated that the stem *Sutcliffia* should be restricted to the Parispermaceae. Accordingly, they had to suppose that the *Sutcliffia* described earlier by SCOTT (1906) and DE FRAINE (1912) from lower stratigraphic horizons might be related to *Paripteris*. A difficulty was that no emergences had been mentioned in either of these older cases. However, these emergences are randomly distributed, and not always present on all peels, even for the type specimen of *S. insignis* var. *tuberculata* (PHILLIPS & ANDREWS, 1963, p. 35). Moreover, the outer parts for the SCOTT and DE FRAINE specimens are poorly preserved. Furthermore, this character is variable and such emergences can be rare on some compressions. The conclusion of LAVEINE *et al.* is, therefore, hypothetical, and can of course be contested, but were it to be incorrect there would be consequences at different levels, as detailed below.

IV.2.4. The *Sutcliffia* - *Paripteris* relationship at a general level

The question of this relationship can be settled independently of any reference to a described permineralized specimen. With a total morphological similarity in all their parts, except for the venation (open or reticulate), and with the certainty that *Linopteris* has a stem structure of *Sutcliffia* type, can it be reasonably supposed that *Paripteris* might have a different stem structure? If the answer is yes, then one must be clearly aware of the fundamental consequences of such a position. It would imply that there can be a total disconnection between the anatomical internal features and the morphological external features. In that case, on which basis should it be postulated that one category of argument is more safe than the others for establishing the relationships between the taxa? Furthermore, there would be no reason why such a discrepancy between anatomical and morphological features should be restricted only to the Parispermaceae! Consequently, all the phylogenetic schemes, may they be based on cladistics, or on any other qualitative or quantitative methods, would all be highly contestable. One can easily imagine all the additional speculative comments that might be developed in such an hypothesis.

IV.2.5. The eventual relationships of the *Sutcliffia insignis*, non *tuberculata*

From the preceding comments, and with the relationship between *Sutcliffia* and *Reticulopteris* mentioned by PHILLIPS & DiMICHELE (1998), the question arises concerning the possibility that some permineralized

rachises of *Sutcliffia* may be fundamentally devoid of any emergences. Such specimens consequently would correspond, in a compressed state, only to those rachises that are longitudinally striated (*Aulacopteris* type), which are known for many different taxa of medullosan pteridosperms. In such a case, it has to be inferred that even if PHILLIPS & DiMICHELE are not followed in their doubt concerning the STIDD *et al.*, 1975 conclusion, they might not be obligatorily wrong in their proposal concerning the correspondence between *Sutcliffia* and *Reticulopteris muensteri*. In this respect it deserves notice that such a correlation is also mentioned by REMY & REMY (1977, p. 117), but unfortunately without any reference or comment sustaining such an affirmation. However, if such an attribution is accurate, it would also mean that, except for the presence or absence of external emergences, two genera (*Linopteris* and *Reticulopteris*), known to differ strongly in their external morphological features, might exhibit totally similar stem structures. In that case, it would have to be concluded that it is impossible to correlate any specific foliage type with permineralized *Sutcliffia insignis* stems when such stems are devoid of connected petioles. This would add to the already known difficulty assigning different kinds of pteridosperm foliage to anatomically preserved *Medullosa* stems. On the other hand, owing to the numerous morphological similarities existing between *Reticulopteris* and *Neuropteris*, it might be supposed that such a conclusion concerning the possibility of having a *Sutcliffia* stem structure might be extended to several other Neuropterid taxa. Ultimately, this would also imply that the basis for the distinction between *Medullosa* and *Sutcliffia insignis* non *tuberculata* stems is clearly not correlatable with morphological variation as distributed among fronds, and consequently that all the anatomical arguments on which the generic distinction was based have to be strongly contested, and revised (TAYLOR & TAYLOR, 1993, p. 526). And once more, there is no argument that would allow us to postulate that such a general conclusion would have to be restricted solely to the Medullosales!

V. CONCLUSION

In recent years, some emphasis has been laid on the significant differences between coal floras (based on palynological and coal ball analyses) and roof floras (DiMICHELE *et al.*, 1996; GASTALDO *et al.*, 1996). It was for instance mentioned that the species richness of the roof floras was nearly twice as large as species richness estimates from coal ball studies (DiMICHELE *et al.*, 1996), and various palaeoecological conclusions were inferred. Although these palaeoecological conclusions are relying on various approaches, and can be considered as validly established, it remains nevertheless

that some biases are clearly introduced by the lack of taxonomical certainties related to Medullosales. Furthermore, even if the biases of over- and under-production of palynomorphs are accounted for in the related palynological studies, it remains that those Medullosales that produce large *Monoletes* pollen grains are not represented in palynological preparations, because of the size of the meshes of the sifters. And it can be added, owing to their restricted distinctive characteristics, that there is little chance that the pollen grains produced by the Parispermaceae may be easily distinguished from some pteridophytic spores through current palynological analyses.

From the above short comments, it appears evident once more that the taxonomic level is the fundamental key for any of the other developments in palaeontological research. It is of course a truism, but it is better to over-emphasize this point than to forget it.

The question of the distinction between *Reticulopteris* and *Linopteris* could appear at first sight to be of rather restricted interest. From the argument developed above, maybe it is not exactly the case. It would now be fundamental to search for permineralized material indisputably associated with *Reticulopteris* foliage, in order to decipher precisely the anatomical characteristics of the taxon, and to estimate its possible relationships.

Because of the confusion between *Linopteris* and *Reticulopteris* in the compression state, it is difficult to settle the precise vertical ranges of these taxa in the U.S.A. Some precise indications on that point might have been of some help in solving the taxonomic question. In Europe, where the vertical range seems to be reliably established, *Reticulopteris muensteri* does not extend beyond the mid-Westphalian D. However, the range of *Reticulopteris* in North America remains to be established precisely, and could be problematic given that other taxa ending in the Westphalian of Europe, including such common species as *Macroneuropteris scheuchzeri* (HOFFMANN), extend well into the Stephanian in North American rocks. The Springfield Coal is at most of late Westphalian D age and, thus, may be above the recognized general range of *Reticulopteris*. If such is the case, it would therefore favor an attribution to *Linopteris*. All these questions being answered, only then will it be well-founded to present additional comments on various points. For instance, REIHMAN & SCHABILION (1978), on the basis of the anatomical adaptations exhibited by a few pinnules preserved in a coal ball, arrived at the conclusion that *R. muensteri* was probably growing in moist environments characterized by favorable osmotic potentials and high humidity. Such a conclusion might be supported by the fact that it is rather usual to find *Reticulopteris* foliage commonly bearing small coiled tubes of *Spirorbis* (Pl. III, fig. 5, 6, 7a, 8). On another hand, ZODROW & CLEAL (1993), on the precise example of *R. muensteri*, have proposed some tentative explanations concerning the eventual link

between the development of anastomosed venation and the establishment of drier climate. Using this logic, *R. muensteri* may have disappeared from lowland basins (either by extinction or by migration to extrabasinal areas) during mid-Westphalian D times because of a reversion to wet conditions. Of course it is always possible to invoke some ecological partitioning within the habitats to explain results that do not exactly fit with the standard scheme. Let us notice, however, that the vertical range of *Linopteris* is larger than that of *Reticulopteris*, and *Linopteris* does not disappear in response to supposed climate changes. These conflicting patterns point out, once more, the danger of over-generalization in this kind of problem; clearly, it could be very easy to expand such speculations.

Now that the main external morphological characteristics of *Linopteris* and *Reticulopteris* are reliably deciphered, it seems most useful at present to direct our efforts toward establishment of the precise vertical range, geographic distribution, and relationship between permineralized and compression specimens throughout North America. Once such information is reliably developed, other considerations regarding evolutionary and ecological patterns can be addressed with greater confidence.

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