# A redescription of the Stephanian species
# *Callipteridium virginianum* (Fontaine & White, 1880) comb. nov.
# and *Alethopteris leonensis* Wagner, 1964

## R.H. Wagner & C. Álvarez-Vázquez

Robert H. Wagner & Carmen Álvarez-Vázquez, Centro Paleobotánico, IMGEMA-Jardín Botánico de Córdoba, Avenida de Linneo, s/n, 14004 Córdoba, Spain (cr1wagro@uco.es).

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An analysis of *Alethopteris virginiana* Fontaine & White from the lower Dunkard in the Appalachians of North America shows that three different taxa are likely to be represented in the initial illustration. The specific epithet '*virginiana*' ought to be restricted to a form comparable to *Callipteridium costei* (Zeiller) Wagner, whereas the two other taxa are referred to pecopterid ferns. A neotype is proposed for *Callipteridium virginianum* (Fontaine & White) comb. nov. on the basis of topotypes. Zeiller's illustration of '*Alethopteris*' *costei* is reproduced for comparison. On the other hand, a full description and illustration are provided for *Alethopteris leonensis* Wagner, a species which had been identified previously with *Alethopteris virginiana*, apparently in error. An associated *Holcospermum* 'seed' is also illustrated. Comparisons include the rather similar *Alethopteris bohemica* Franke, 1912, which is also illustrated with an associated 'seed'. The age of the lower Dunkard flora is determined as (early?) Autunian. The relative position of the Upper Pennsylvanian (upper Conemaugh, Monongahela, Dunkard) of eastern North America is depicted in a chart showing the full succession of substages in the West European chronostratigraphic classification of the Pennsylvanian Subsystem, as well as the corresponding megafloral zones.

## Contents

## Dedication

In contributing to a volume honouring Cor Winkler Prins it seems appropriate to do so with a topic related to the Cantabrian Mountains in northwest Spain. Not only has this been an area of major activity by Cor, but the senior author of the present paper looks back with pleasure on four decades of fruitful collaboration and continuing with the person to whom this volume is dedicated. It is not only the conjunction of different

kinds of expertise, but the personal friendship which has contributed to a harmonious collaboration. May this be testimony of a lasting appreciation, with which the junior author concurs wholeheartedly.

## Introduction

The fossil floras of the Carboniferous in Spain have only been studied comprehensively from the second half of the 20th Century onwards. The initial impetus for this resurgence of interest was provided by Jongmans (1951), who analysed the (rather exiguous) records in the literature and commenced large-scale collecting. His endeavours were supported by the Consejo Superior de Investigaciones Científicas (CSIC) through the good offices (and collaboration) of Prof. B. Meléndez at the University of Madrid. Since then, numerous papers have been published, including several memoirs providing the detailed taxonomic treatment of a large number of species. An historical account of the investigations was published by Wagner (2005), and a general synthesis of the Carboniferous floras in Spain and Portugal has been prepared by Wagner & Álvarez-Vázquez (2010). These floras are now quite well known.

Most remarkable is the almost complete record of Stephanian floras in northwest Spain, with a gradual transition from the Asturian (ex Westphalian D), upwards into Cantabrian, Barruelian, Saberian and Stephanian B substages. Higher Stephanian substages (Stephanian C, Autunian *sensu stricto*) are also represented in northwest Spain, albeit with much more sporadic floral records. Indeed, the Stephanian C and Autunian substages are represented by more adequate floral records in central and southwestern Spain (Wagner & Álvarez-Vázquez, 2010). The upper Asturian, Cantabrian and lower Barruelian succession occurs with *c*. 6,000 m of strata in partly marine and partly terrestrial facies in the southeastern part of the Cantabric-Asturian arcuate fold belt. These constitute a unique record (Wagner & Winkler Prins, 1985; Wagner *et al*., 2002), because this interval is much less completely developed, with several stratigraphic gaps, in different parts of northern Europe and eastern North America. Subsequent upper Barruelian, Saberian and Stephanian B strata, reaching a cumulative total of almost 7,000 m, were laid down in a successor basin in the Cantabric-Asturian arcuate fold belt (Cantabrian Mountains) in northwest Spain. These provide a comprehensive record of megafloral remains, allowing correlation with the more patchily developed classic Stephanian successions in the various intramontane basins of the Massif Central (south-central France).

Correlations with the Appalachian area of eastern North America (Wagner & Lyons, 1997) suggest a sizeable gap in the Stephanian record of this area (Fig. 1). An equally important (similar) gap occurs in the palaeogeographically continuous area of the Paralic Coal Belt in northern Europe. This is still in need of a comprehensive, published analysis. The size of this stratigraphic gap in the Paralic Coal Belt succession only became apparent when the more complete floral succession in northwest Spain was studied in detail. It is also noted that the gradual nature of floral changes in the up to 10,000 m thick Stephanian (up to Stephanian B) succession in northwest Spain, which may be the most complete in the world, suggests that the oft-repeated assertion of a sudden floral change at the Middle-Upper Pennsylvanian boundary (often equated, wrongly, with the Westphalian-Stephanian boundary) needs to be questioned. Reference is made, in

the first instance, to Phillips & Peppers (1984), who recorded a marked change from lycopod rich Desmoinesian coals to tree fern dominated Missourian coals in Illinois, U.S.A. The suddenness of this changeover was ascribed to a fairly dramatic climatic change (see also DiMichele *et al.*, 2001), but if a sizeable time gap is involved (Wagner & Lyons, 1997), this climatic change may have been much more gradual than these authors suggested. A reappraisal is in order. Indeed, the existing controversy can only be solved when the elements for detailed correlation are in place. This requires well studied floral successions in the higher Pennsylvanian of northern Europe and eastern North America, as well as in the Iberian Peninsula. It goes without saying that the proper identification of megafloral taxa is basic to a proper evaluation of these floral successions. (Microfloras are less determinative in Stephanian strata than they are in the Namurian-Westphalian; Wagner, 1984, pp. 112-113.)

The present paper focuses on two taxa, *Alethopteris virginiana* and *Alethopteris leonensis*, which Gillespie & Pfefferkorn (1986) regarded as synonymous. The former was described from the Dunkard beds in West Virginia, U.S.A., whilst the latter was recorded

| SERIES | | GLOBAL STAGES | SUBSTAGES (W. Europe) | Megafloral zones | R. STAGES | Central Appalachian lithostratigraphy |
|---|---|---|---|---|---|---|
| P E N N S Y L V A N I A N | UPPER | GZHELIAN | middle to upper Autunian | *A. spicata* | STEPHANIAN | Dunkard Monongahela Conemaugh |
| | | | Stephanian C (= lower Autunian) | *A. conferta* | | |
| | | KASIMOVIAN | Stephanian B | *Sph. angustifolium* | | G A P |
| | | | "Saberian" | *A. zeilleri* | | |
| | | | Barruelian | *L. lamuriana* | | |
| | | | Cantabrian | *O. cantabrica* | | |
| | MIDDLE | MOSCOVIAN | Asturian | *L. vestita* | WESTPHALIAN | Conemaugh * Allegheny |
| | | | | *L. obliqua* | | G A P ? |
| | | | Bolsovian | *P. linguaefolia* | | Kanawha |
| | | | Duckmantian | *L. rugosa / A. urophylla* | | |
| | | | Langsettian | *L. hoeninghausii / N. schlehanii* | | New River |
| | LOWER | BASHKIRIAN | Yeadonian | *N. larischii / P. aspera* | NAMURIAN (*pars*) | Pocahontas |
| | | | Marsdenian | | | G A P |
| | | | Kinderscoutian | | | |
| | | | Alportian | | | |
| | | | Chokierian | | | |

**\* up to and including Mahoning coal where preserved**

Fig. 1. Chronostratigraphic divisions of the Pennsylvanian Subsystem (Carboniferous), with correlations regarding the West European regional chronostratigraphic units (stages and substages) and the lithostratigraphic units of the Appalachian region, North America, shown alongside megafloral zones as published by Wagner & Álvarez-Vázquez (2010).

from the Stephanian of the Cantabrian Mountains, northwest Spain. The first author has been privileged to collect with Bill Gillespie from a locality in the type area of *Alethopteris virginiana*, thus providing first hand acquaintance with the form identified as such. Only fragmentary, but quite typical specimens of *Alethopteris virginiana* were collected (and identified *in situ* by W.H. Gillespie), whereas fairly abundant additional material of *Alethopteris leonensis* was collected more recently from Stephanian B strata in the Villablino Coalfield of northern León in the Cantabrian Mountains. A comparative analysis of both taxa can thus be based on material from the representative type areas.

## The Dunkard problem

In the context of the present paper, it is relevant to date the lower Dunkard of West Virginia (containing *Alethopteris virginiana*) and to discuss the circumstances surrounding the floral record from this part of the Upper Pennsylvanian succession (as defined by the U.S. Geological Survey). The memoir by Fontaine & White (1880) on the Dunkard flora is most important in this respect. It is noted that this memoir has raised several doubts, as expressed in the literature, mainly because of the rather diagrammatic nature of its illustrations, but also because the original specimens figured and described are no longer available. It is of more than historical interest that David White (1904) compared the Dunkard flora with that of the German Rotliegend (Lower Rotliegend equals Autunian). Equally relevant is the fact that the floral records from the upper Conemaugh, Monongahela and basal Dunkard (together constituting the Upper Pennsylvanian of U.S.G.S.) are quite similar, as several authors have pointed out, and which is confirmed by Wagner & Lyons (1997) and Blake *et al.* (2002). It is also noted that Darrah (1969, p. 26) observed "a marked floral break
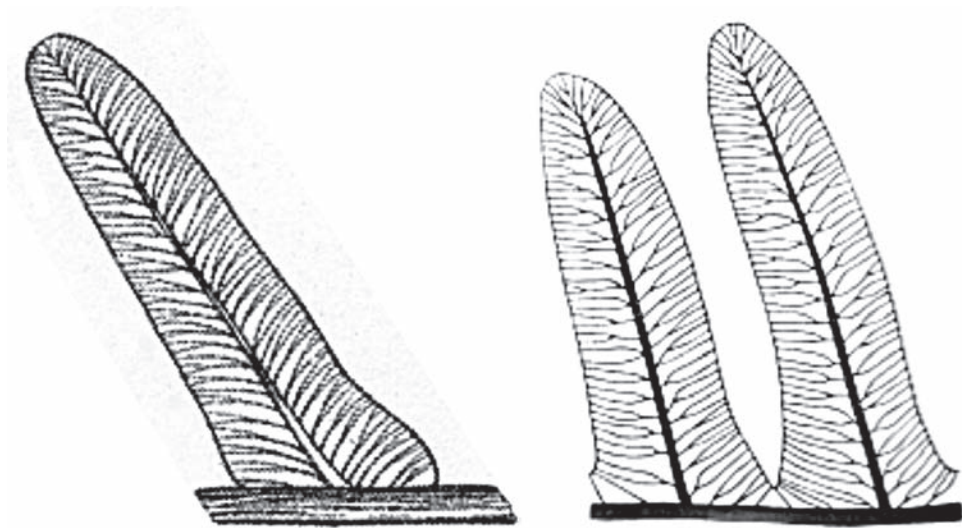


Fig. 2. Venation diagrams (× 3) of (A) *Callipteridium virginianum* from lower Dunkard in the Appalachians and (B) *Alethopteris leonensis* from the Stephanian of northwest Spain (after Fontaine & White, 1880, pl. 33, fig. 4a, and Wagner, 1968, text-fig. 21, respectively).

in the mid-Conemaugh", an observation which is supported by the evidence discussed by Wagner & Lyons (1997). It is here suggested that the upper Conemaugh, Monongahela and lower Dunkard may be generally equivalent to the Autunian of western Europe, leaving open the possibility that the upper part of Stephanian B may be included as well (although this is regarded as unlikely). The correlation (Fig. 1) reflects recent precision in the recognition of Stephanian substages (Wagner & Álvarez-Vázquez, in press).

The floral break noted by Darrah (1969) and evaluated in more detail by Wagner & Lyons (1997) is also admitted by Blake *et al.* (2002) even though the latter authors regarded it as more minor. Indeed, the range chart published by the latter authors (fig. 2 therein) shows a number of extinctions and new appearances above the upper Freeport coal (roof shales) (lower Conemaugh) and below the Brush Creek coal (upper Conemaugh), in West Virginia and the adjacent part of Maryland. Stratigraphically important taxa recorded from the upper Conemaugh in Ohio (Wagner & Lyons, 1997) include *Danaeites emersonii* Lesquereux, *Lobatopteris geinitzi* (Göppert) Wagner, *Annularia spicata* Gutbier, and *Taeniopteris* cf. *multinervia* Weiss (= *Taeniopteris abnormis* Gutbier). The records in Blake *et al.* (2002) add *Diplazites emarginatus* Göppert and *Sphenophyllum angustifolium* Germar at the level of the Pittsburg coal, low in the Monongahela. *Walchia piniformis* Schlotheim *ex* Sternberg occurs throughout. These taxa are not out of place with the lower Dunkard flora, as described by Fontaine & White (1880). A very high level in the Stephanian Stage of western Europe is suggested by these floral records, that is, the *Autunia conferta* and *Annularia spicata* zones of Wagner & Álvarez-Vázquez (in press). Whether or not the upper part of the *Sphenophyllum angustifolium* Zone is represented should be examined in future with more detailed records. Since the Upper Freeport roof shales represent basal Cantabrian (by common consent), a large part of the Stephanian Stage would be missing in most of eastern North America (with the possible exception of the Narragansett Basin; see Wagner & Lyons, 1997). The same observation applies for the Maritime Provinces of Canada and the Paralic Coal Belt of northern Europe, thus suggesting a large-scale regional uplift and erosion prior to the deposition of Lower Rotliegend. We focus on the Appalachian record herein, with special regard to the lower Dunkard.

The large time gap deduced by Wagner & Lyons (1997) below the upper Conemaugh, Monongahela and Dunkard succession was reduced to only part of the lower Stephanian in a discussion by Blake *et al.* (2002), apparently because physical evidence of a major break in succession had not been seen. Blake *et al.* (2002, p. 275) tried to explain part of the problem by regarding the Spanish floral record (meaning the Cantabrian Mountains of northwest Spain) as containing many endemic forms. However, this is a very unlikely explanation. The Stephanian megafloral record in northwest Spain originates from coastal basins on the edge of the Palaeotethys. This is not a scenario for endemism. The large amount of floral diversity in the Stephanian of northwest Spain also does not suggest endemism, but quite the contrary. It is further noted that the palaeogeographic reconstructions as quoted by Blake *et al.* (2002) are rather questionable, reflecting an inadequate knowledge of the Carboniferous geology of the Iberian Peninsula. Additional, more general considerations by Blake *et al.* (2002, p. 276) are generally correct, but seem irrelevant in the context in which they have been quoted. Blake *et al.* (2002) obviously regarded the conclusions reached by Wagner & Lyons

(1997) as unwelcome in the light of interpretations current in the North American literature. A detailed comparison between the floral succession in northwest Spain and that of the Appalachian area is obviously required.

If the (upper) Conemaugh flora from Ohio, discussed and partly figured by Wagner & Lyons (1997), contains elements of the *Annularia spicata* Zone, it would place most of the Conemaugh, the Monongahela and the Dunkard already as high as the middle to upper Autunian, that is, Autunian *sensu stricto* (Fig. 1), in the highest Stephanian, right at the top of the Pennsylvanian Subsystem. In this case, most of the classical Stephanian succession would be absent from the Appalachian record. Although this may well be true, further substantiation is desirable.

Blake *et al*. (2002, pp. 272-273) discussed upper Conemaugh, Monongahela and lower Dunkard floras, but the most important floral record remains that published by Fontaine & White (1880), who figured and described mainly specimens from the basal Dunkard, that is, the Waynesburg coal horizon. As mentioned already, the main problem lies with the quality of Fontaine & White's illustrations. Although their drawings provide an adequate impression of the general morphology, they do not seem to depict the venation in precise detail. Fontaine & White had access to large specimens which seem to have been quite well preserved. However, the collection on which Fontaine & White's paper was based, was reported as having been destroyed in a fire (Cross, 1958). This is a serious mishap, because there is no record of any collections of similar quality being available at present and it is necessary to reconsider the obsolete determinations by Fontaine & White. An early attempt at revision was published by White (1904), in a brief note which was aimed, primarily, at judging the age of the Dunkard flora. It is recalled that Fontaine & White (1880), rather evocatively, labelled their memoir *The Permian or Upper Carboniferous Flora*. This initiated a controversy which White (1904) tried to resolve by concluding that "The Dunkard plants indicate the presence in the Appalachian trough of a transition from the Coal Measures to the typical Permian floras". David White also referred to the 'Rotliegend' (Lower Rotliegend in particular) which he seems to have equated with the basal Permian, in agreement with common opinion at his time of writing, over a century ago. The stratigraphic problem was debated extensively in a special symposium on *The Age of the Dunkard* held in 1972 (Barlow, 1975).

Fontaine & White's list of species from the basal Dunkard (Cassville Shales/Waynesburg Coal) was quoted in full by Darrah (1969), who noted that the 60 species recorded were excessive, but refrained from naming synonyms (as David White had done, albeit with only a few examples).

In *The Age of the Dunkard*, Darrah (1975) focused on the so-called Permian elements in the (upper) Conemaugh, Monongahela and Dunkard floras, for which he quoted *Ernestiodendron* cf. *piniformis* (probably a misquote) and *Walchia* sp. It was intriguing that Darrah (1975, p. 85) queried the report that Fontaine & White's collection would have been destroyed in a fire (doubts which were expressed also by Watt in an unpublished manuscript). Whatever happened, the fact remains that the whereabouts of Fontaine & White's collection are unknown (W.A. DiMichele, pers. comm.).

Perhaps the most important account of the Dunkard flora was given by Gillespie *et al*. (1975), who proposed a number of synonyms, but stopped short of a full revision. They considered that *Callipteridium dawsonianum* Fontaine & White and *Callipteridium*

*grandifolium* Fontaine & White would represent the pecopterid fern *Danaeites emersonii*. This is almost certainly correct and it may be that part of the material figured as *Callipteridium oblongifolium* Fontaine & White (but excluding their pl. 12, figs 2, 2a) also belongs to this species. Although more doubtful, this might apply also to *Pecopteris asplenioides* Fontaine & White. Gillespie *et al.* (1975) also queried the records of *Saportaea* Fontaine & White and *Baiera* Braun, removing these taxa from the Dunkard flora. Furthermore, they proposed that *Nematophyllites* Miller (= *Nematophyllum* Fontaine & White) should be replaced by *Asterophyllites longifolius* (Sternberg) Brongniart, a conclusion which is not immediately apparent from the illustrations in Fontaine & White's memoir. Gillespie *et al.* (1975, p. 229) further mentioned that Cross (1958) was inclined to group several of Fontaine & White's pecopterid species into a mere dozen taxa, thus casting severe doubt on the accuracy of Fontaine & White's specific descriptions. Additional comments by Gillespie *et al*. (1975) included a fairly extensive one on *Alethopteris virginiana* and its association with the male synangium *Dolerotheca*.

Wagner & Lyons (1997) also attempted to recognise some of Fontaine & White's taxa. They figured *Mixoneura nervosa* (Fontaine & White) Wagner & Lyons from the upper Conemaugh of Ohio, combining this species with *Odontopteris obtusiloba* var. *rarinervis* Fontaine & White. They also recognised *Lobatopteris tenuinervis* (Fontaine & White) Wagner and figured material identified as *Pecopteris platynervis* Fontaine & White. Similar specimens to *P. platynervis* were figured from Stephanian C (= lower Autunian) strata in the Puertollano Coalfield, central Spain (Wagner, 1985, 1999).

Although several species described by Fontaine & White (1880) may be identifiable, the total flora from the Cassville Shale (parting and roof shales) of the Waynesburg coal seam in the lower Dunkard can only be analysed with the aid of new material of comparable quality to that available to the original authors. Where only fragmentary specimens are available for redescription, a certain amount of conjecture is inevitable in view of the diagrammatic nature of the original illustrations. Reinterpretations of Fontaine & White's (1880) identifications are discussed as follows (only a selection of species is commented on since some of the illustrations do not allow easy recognition).

*Neuropteris odontopteroides* **Fontaine & White** (1880, pl. 9, figs. 1-6). Possibly the same as *Neuropteris zeilleri* de Lima, which might be a synonym. It may be that *Neuropteris flexuosa* Brongniart var. *longifolia* Fontaine & White, pl. 8, figs. 1, 6, and *Neuropteris platynervis* Fontaine & White, pl. 8, fig. 2, should also be included.

**cf.** *Macroneuropteris scheuchzeri* **(Hoffmann) Cleal** *et al.* = *Neuropteris hirsuta* Lesquereux as figured by Fontaine & White, 1880, pl. 8, figs. 7-8, a doubtful record (see Gillespie *et al*., 1975, p. 228).

*Mixoneura nervosa* **(Fontaine & White) Wagner & Lyons**, incorporating *Odontopteris nervosa* Fontaine & White, 1880, pl. 10, figs. 1, 2; *Odontopteris densifolia* Fontaine & White, 1880, pl. 10, fig. 3; and *Odontopteris obtusiloba* var. *rarinervis* Fontaine & White, 1880, pl. 10, figs. 1-4.

*Barthelopteris germari* **(Giebel) Zodrow & Cleal** = *Neuropteris dictyopteroides* Fontaine & White, 1880, pl. 8, figs. 3-5 – assigned with doubt to *Dictyopteris schuetzei* Römer by Potonié, 1893, p. 144, a synonym of *Barthelopteris germari*.

**?*Alethopteris bohemica* Franke** = *Alethopteris gigas*? Gutbier as figured by Fontaine & White, 1880, pl. 33, figs. 5, 6 – determined on pinnule shape only; no venation seems to have been preserved.

***Callipteridium (Praecallipteridium) virginianum* (Fontaine & White) comb. nov.** = *Alethopteris virginiana* Fontaine & White, *pars*, 1880, pl. 33, figs. 1-4; perhaps also pl. 32, figs. 3, 5. (See below.)

***Pseudomariopteris cordato-ovata* (Weiss) Gillespie *et al.*** = *Odontopteris pachyderma* Fontaine & White, 1880, pl. 10, figs. 5-10; also *Callipteridium* sp. as figured by Fontaine & White, 1880, pl. 11, figs. 5, 7 (*non* fig. 6 which may represent *Oligocarpia*). David White (1904) compared *Odontopteris pachyderma* with *Diplotmema ribeyronii* Zeiller, a later synonym of *Pseudomariopteris cordato-ovata*.

***Taeniopteris* cf. *abnormis* Gutbier** = *Taeniopteris newberriana* Fontaine & White, 1880, pl. 34, figs. 1-8, and *Taeniopteris lescuriana* Fontaine & White, 1880, pl. 34, figs. 9, 9a.

**?*Dicksonites plukenetii* (Schlotheim *ex* Sternberg) Sterzel** = *Pecopteris goniopteroides* Fontaine & White, 1880, pl. 25, figs. 2, 2a.

***Discopteris acrocarpa* (Fontaine & White) comb. nov.** Basionym: *Sphenopteris acrocarpa* Fontaine & White, *pars*, 1880, pp. 40-41, pl. 3, figs. 1-3; pl. 4, figs. 1-5. Lectotype designated herein as Fontaine & White, 1880, pl. 3, fig. 2.

***Oligocarpia gutbieri* Göppert** = *Pecopteris pennaeformis* Brongniart as figured by Fontaine & White, 1880, pl. 17, figs. 4-5a; also *Pecopteris rotundiloba* Fontaine & White, 1880, pl. 17, figs. 2, 2a; as well as *Pecopteris germari* Weiss as figured by Fontaine & White, 1880, pl. 19, figs. 1-7.

***Renaultia lebachensis* (Weiss) Brousmiche** = *Sphenopteris minutisecta* Fontaine & White, 1880, pl. 5, figs. 1-4.

***Sphenopteris lescuriana* Fontaine & White,** 1880, pl. 6, figs. 1-1b; pl. 7, figs. 1-2 – comparable to *Renaultia lebachensis*, but showing larger size pinnules.

***Sphenopteris auriculata* Fontaine & White** (1880, pl. 7, figs. 3, 4) is very similar to *Sphenopteris lescuriana*, perhaps the same species. Blake *et al*. (2002, p. 276) identified it with *Prynadaeopteris anthriscifolia* Radczenko (*sensu* Broutin, 1986), referring to a pinna fragment from the Autunian of Guadalcanal, in southwest Spain, which the present writers prefer to compare with *"Pecopteris" tenuicostata* Halle, 1927, from the Permian of China.

**cf. *Pseudomariopteris busquetii* (Zeiller) Danzé-Corsin** = *Sphenopteris heeriana* Fontaine & White, 1880, *pars*, pl. 25, figs. 3-6a, also to be compared with *Helenopteris paleaui* (Zeiller) Krings & Kerp; *non* pl. 25, figs. 7, 7a = *Senftenbergia gruneri*? (Zeiller) Wagner & Álvarez-Vázquez.

***Discopteris pachypteroides* (Fontaine & White) comb. nov.** Basionym: *Pecopteris pachypteroides* Fontaine & White, 1880, p. 76, pl. 26, figs. 1-4. Lectotype designated herein as Fontaine & White, 1880, pl. 26, fig. 1 – comparable to *Sphenopteris taiyuanensis* Halle, 1927, and *Sphenopteris durbanensis* Corsin & Vila, 1963, which is almost certainly a *Discopteris*. Blake *et al*. (2002, pl. 5, fig. 2) figured *Sphenopteris durbanensis* from the Waynesburg Coal.

***Danaeites emersonii* Lesquereux** = *Callipteridium oblongifolium* Fontaine & White, 1880, *pars*, pl. 12, figs. 1, 3-5; *non* pl. 12, figs. 2, 2a = *Pecopteris* sp. indet.; also *Callipteridium dawsonianum* Fontaine & White, 1880, pl. 13, figs. 1, 2, pl. 14, figs. 1, 1a; *Callipteridium grandifolium* Fontaine & White, 1880, pl. 15, figs. 1-4a, pl. 16, figs. 2-4; and possibly also *Pecopteris asplenioides* Fontaine & White, 1880, pl. 25, figs. 1, 1a.

***Diplazites emarginatus* Göppert** = *Goniopteris oblonga* Fontaine & White, 1880, *pars*, pl. 30, figs. 4, 4a; *non* pl. 30, figs. 3, 5 = *Diplazites* sp.

***Diplazites* sp.** = *Goniopteris oblonga* Fontaine & White *pars*, 1880, pl. 30, figs. 3, 5; also *Goniopteris elliptica* Fontaine & White, 1880, pl. 30, figs. 1, 1a.

***Nemejcopteris feminaeformis* (Schlotheim *ex* Sterzel) Barthel** = *Goniopteris newberriana* Fontaine & White, 1880, pl. 30, figs. 2, 2a; possibly also *Cymoglossa formosa* Fontaine & White, 1880, pl. 31, figs. 1-2.

***Senftenbergia gruneri* (Zeiller) Wagner & Álvarez-Vázquez** = *Pecopteris dentata* Brongniart as figured in Fontaine & White, 1880, pl. 32, figs. 1-5; possibly also *Sphenopteris heeriana* Fontaine & White, 1880, *pars*, pl. 25, figs. 7, 7a.

***Lobatopteris tenuinervis* (Fontaine & White) Wagner** = *Pecopteris tenuinervis* Fontaine & White, 1880, pl. 28, figs. 1-4; also *Pecopteris candolleana* Brongniart as figured by Fontaine & White, 1880, pl. 20, figs. 1-3; and *Pecopteris imbricata* Fontaine & White, 1880, pl. 23, figs. 1, 1a, a homonym of *Pecopteris imbricata* (Göppert) Radczenko; also, perhaps, *Cymoglossa breviloba* Fontaine & White, pl. 31, figs. 3, 3a; and *Alethopteris virginiana* Fontaine & White, 1880, *pars*, pl. 32, fig. 2.

***Lobatopteris schimperiana* (Fontaine & White) comb. nov.** Basionym: *Pecopteris schimperiana* Fontaine & White, 1880, p. 75, pl. 24, figs. 1-5. Lectotype designated herein as Fontaine & White, 1880, pl. 24, figs. 1, 1a (the same as *Lobatopteris viannae* (Teixeira) Wagner). White (1904) compared *Pecopteris schimperiana* with *Pecopteris bredovii* Gutbier (an *Oligocarpia*), but this is here regarded as incorrect. It might be that *Pecopteris rarinervis* Fontaine & White (1880, pl. 20, figs. 6-8) should also be referred to *Lobatopteris schimperiana* = *Lobatopteris viannae*, but the quality of the illustrations does not allow a definitive conclusion. White (1904) compared with *Pecopteris* (now *Remia*) *pinnatifida* Gutbier, but this seems to have been in error.

**cf. *Polymorphopteris subelegans* (Potonié) Wagner** = *Alethopteris virginiana* Fontaine & White, 1880, *pars*, pl. 32, figs. 1, 1a, 4.

*Pecopteris merianopteroides* **Fontaine & White**, 1880, pl. 29, figs. 1-2a (comparable to *Pecopteris monyi* Zeiller, but possibly not this species).

*Pecopteris platynervis* **Fontaine & White** *pars*, excluding Fontaine & White's pl. 18, figs. 6, 6a, which seem more comparable to *Polymorphopteris subelegans* (Potonié) Wagner.

*Aphlebia crispa* **Gutbier** *auct.* = *Rhacophyllum filiciforme* var. *majus* Fontaine & White, 1880, pl. 35, fig. 1.

*Sphenophyllum angustifolium* **Germar** = *Sphenophyllum tenuifolium* Fontaine & White, 1880, pl. 1, figs. 9, 9a. *Sphenophyllum tenuifolium* was maintained as a separate species by Abbott (1958).

*Sphenophyllum oblongifolium* **(Germar & Kaulfuss) Unger** = *Sphenophyllum densifoliatum* Fontaine & White, 1880, pl. 1, figs. 7, 7a, and *Sphenophyllum filiculmis* Lesquereux as figured in Fontaine & White, 1880, pl. 1, figs. 8, 8a.

*Sphenophyllum* **sp. indet.** = *Sphenophyllum latifolium* Fontaine & White, 1880, pl. 1, figs. 10, 11 – leaves with damaged margins, possibly comparable with *Sphenophyllum verticillatum*. (*Sphenophyllum latifolium* Fontaine & White is a homonym of *Sphenophyllum latifolium* Wood, 1869, a different species which is probably synonymous with *Sphenophyllum alatifolium* Renault.)

*Sigillaria brardii* **Brongniart** = *Sigillaria approximata* Fontaine & White, 1880, pl. 37, fig. 3.

It is clear that judging Fontaine & White's drawings is sometimes a guessing game. Some of their taxa are difficult, if not impossible, to identify properly. This applies most obviously to the sphenopterid ferns, which require exquisite detail to be identifiable at the species level. However, the selected list of species serves to confirm the suspicion that the Waynesburg coal horizon contains an Autunian flora, at least as high as Stephanian C (= lower Autunian). This conclusion agrees with a slightly later age (= mid to late Autunian), that is, Autunian *sensu stricto*, of the Washington coal, higher in the Dunkard succession, where *Autunia conferta* (Sternberg) Kerp and *Autunia naumannii* (Gutbier) Kerp (= *Sphenopteris coriacea* Fontaine & White) have been found. Although Cross (1958) attributed this latter species to *Callipteris lyratifolia* (Göppert) Grand'Eury (= *Rhachiphyllum lyratifolia* (Göppert) Kerp), an opinion quoted by Gillespie *et al.* (1975, p. 228), this is not accepted by the present writers. Some of the suggestions in the present paper coincide with earlier opinions expressed by White (1904) and, particularly, Gillespie *et al.* (1975). This stratigraphic conclusion allows positioning *Callipteridium virginianum* with regard to the European records of the similar species *Callipteridium costei*, which reaches into the Autunian, and *Alethopteris leonensis* which has its highest occurrence in Stephanian C (= lower Autunian).

**Analysis of *Alethopteris virginiana***
**as figured and described by Fontaine & White, 1880**

It seems that the material figured and described under this name by Fontaine & White (1880) is too varied to be ascribed to a single taxon. The authors themselves (p. 89) mentioned already that "The plant is very polymorphous, so much so indeed, that but for the abundant material afforded, which enables us to obtain a number of inter-mediate forms, we would have been tempted to form several species out of this one". It is unfortunate that Fontaine & White's specimens are no longer available, but the illustrations (drawings) allow certain observations to be made. These are supplemented by direct examination of specimens collected more recently from the Waynesburg Coal.

An examination of Fontaine & White's illustrations suggests that their (pl. 32, figs. 1, 1a, 4) probably belongs to a pecopterid fern attributable to the *Polymorphopteris* group as defined by Wagner (1959a). Part of Fontaine & White's (pl. 32) is reproduced here as Plate 1. It is noted that White (1904) already suggested that *Alethopteris virginiana* should be compared with *Callipteridium subelegans* Potonié, a species introduced by Potonié (1893) from the Lower Rotliegend of Thuringia, Germany. Presumably he referred to Fontaine & White (1880, pl. 32, figs. 1, 1a), in particular. Potonie's species was removed from *Callipteridium* by both Doubinger (1958) and Wagner (1959a), who suggested that it represented a pecopterid fern of the 'polymorpha' alliance, that is, *Polymorphopteris* Wagner. The perpendicular insertion of pinnules with slightly constricted bases as shown in the venation diagram of Fontaine & White (1880, pl. 32, fig. 1a) suggests a *Polymorphopteris*, even though the characteristically four-pronged lateral vein groups are not apparent in the drawing. However, this may be due to indifferent preservation as a result of the lithology (a silty mudstone) of the Cassville Shale parting near the top of the Waynesburg coal. There is no hint of apparent 'subsidiary veins' arising from the rachis and decurrent pinnule bases are conspicuously lacking. These specimens are attributable neither to *Alethopteris* nor *Callipteridium*.

If David White was correct in his attribution of Fontaine & White's (pl. 32, figs. 1, 1a) to *Polymorphopteris subelegans* (Potonié) Wagner, it leaves the problem of a proper recognition of this taxon. According to Barthel (1981), *Alethopteris subelegans* (Potonié) Franke should be subsumed in *Pecopteris* (now *Polymorphopteris*) *pseudobucklandii* Andrae (*in* Germar, 1853). On the other hand, the interpretation of *Polymorphopteris subelegans* by Wagner (1962a, pl. 31, figs. 19, 20) shows a well characterised species which may or may not represent the taxon introduced by Potonié on a couple of pinna fragments. An additional complication (Barthel, 1981) is that Wagner (1959a) figured and described a *Polymorphopteris pseudobucklandii* which did not conform to the type as figured photo-graphically by Remy & Remy (1959). The corresponding material was indeed rede-scribed as *Polymorphopteris magdalenae* Wagner, 1964 (see also Castro, 2005a, pls. 29, 30). Although the possibility exists that Fontaine & White's (1880, pl. 32, fig. 4) should be assigned to *Polymorphopteris subelegans*, this is by no means certain.

On the other hand, the lobate pinna fragment illustrated on Fontaine & White (1880, pl. 32, fig. 2) shows a venation pattern which suggests a *Lobatopteris*. Although it is difficult to assign this specimen properly, it seems that the most likely attribution is to *Lobatopteris tenuinervis* (Fontaine & White) Wagner (see Wagner & Lyons, 1997). Among the various pecopterids figured by Fontaine & White (1880), it may be that the three

specimens which they referred to *Pecopteris candolleana* Brongniart (pl. 20, figs. 1-3) might belong to the same species of *Lobatopteris*. The single specimen depicted as *Pecopteris miltonii* Göppert (Fontaine & White, 1880, pl. 23, figs. 2, 3) might also belong to *Lobatopteris tenuinervis*. With the possible exception of the two small pinna fragments shown by Fontaine & White (1880, pl. 32, figs. 3, 5), which might represent the taxon recorded here as *Callipteridium virginianum*, the specimens illustrated in this plate all seem to belong to pecopterid ferns.

This leaves Fontaine & White's (1880, pl. 33, figs. 1-4a) as the most characteristic representation of *Alethopteris virginiana sensu stricto*, an opinion which is reinforced by the illustration of *Alethopteris virginiana* by Gillespie *et al*. (1975, 1978), Cross *et al*. (1996) and Blake *et al*. (2002). This fairly distinctive form may be identified without too much difficulty. Specimens of this type were collected from the shale parting in the Waynesburg Coal near Cassville. A representative selection of specimens from the Cassville Shale is figured herein (Pl. 4; Pl. 5, figs, 1, 2). Of course, if this form is identified specifically with *Alethopteris virginiana*, a new emended species description is needed as well as the designation of a neotype.

A different issue is its correct generic attribution. It is observed that the pinnules of *Alethopteris virginiana* from the Cassville Shale possess an apparent bilateral symmetry and lack the decurrent base regarded as characteristic for *Alethopteris*. Indeed, there is a much closer resemblance with *Callipteridium*. A marked similarity is noted with *Callipteridium (Praecallipteridium) costei*, a species originally described as *Alethopteris costei* (Zeiller, 1906) from the upper Stephanian of Blanzy in the Massif Central, south-central France. Although never very common, this species is fairly widespread, being found also at Decazeville in the Massif Central (Vetter, 1968), Sabero in the Cantabrian Mountains of northwest Spain (Knight, 1983) and the Breitenbach Formation (Stephanian C) of Saarland (as mentioned by Langiaux, 1984). A fairly exhaustive discussion has been provided by Knight (1983). Part of the type specimen as figured by Zeiller (1906) is reproduced herein (Pl. 3).

A comparison with specimens of *Callipteridium virginianum* (Pl. 4; Pl. 5, figs 1, 2) shows that Zeiller's species is sufficiently close to warrant considering a possible synonymy. If the American and European material is kept separate as two different taxa, for the time being, it is because *Callipteridium virginianum* is not known sufficiently well to establish the intraspecific variability. This is much better known for *Callipteridium costei* which has been analysed by Laveine *et al.* (1977) with regard to intercalated pinnules (absent) and intercalated pinnae (present).

### Systematic palaeontology

*Remarks* – The suprageneric taxonomy used follows that Anderson *et al.* (2007). In the synonymy list the following system of annotations is used (shortened/simplified from Cleal & Shute, 1995): Key: * = the protologue and other illustrations of type(s); ? = references to doubtful specimens due to poor illustration or preservation; p, *pars* = only part of the specimens published belong to the species; v, *vide* = the authors have seen the specimen(s).

**Class Cycadopsida Brongniart, 1843, emend. Anderson *et al.*, 2007**
**Order Medullosales Corsin, 1960**
**Family Alethopteridaceae Corsin, 1960, emend. Anderson *et al.*, 2007**
**Genus *Callipteridum* Weiss, 1870**

*Type species* – *Callipteridium (Eucallipteridium) pteridium* (Schlotheim, 1804, *ex* Zeiller *in* Renault & Zeiller, 1888) Zeiller *in* Renault & Zeiller, 1888.

**Callipteridium (*Praecallipteridium*) *virginianum* (Fontaine & White, 1880) comb. nov.**
Fig. 2A; Pls 2, 4; Pl. 5, figs 1, 2.

* p  1880 *Alethopteris virginiana* Fontaine & White, pp. 88-89, pl. 32, figs. 3, 5(?); pl. 33, figs. 1-4a [*non* pl. 32, figs. 1, 1a, 4 = cf. *Polymorphopteris subelegans* (Potonié) Wagner; *non* fig. 2 (to be compared with *Lobatopteris tenuinervis* (Fontaine & White) Wagner)].
   1978 *Alethopteris virginiana* Fontaine & White; Gillespie *et al.*, p. 101, pl. 36, fig. 2.
   1986 *Alethopteris virginiana* Fontaine & White; Gillespie & Pfefferkorn, p. 25.
   1996 *Alethopteris virginiana* Fontaine & White; Cross *et al.*, p. 412, figs. 23-21, figs. 4-5.
   2002 *Alethopteris virginiana* Fontaine & White; Blake *et al.*, pp. 264, 277, pl. 7, fig. 3; pl. 30, figs. 2, 3.

*Material and repository* – Several pinna fragments from the type area, the Cassville Shale (parting and roof shales of the Waynesburg coal seam), from a road bend near Cassville, West Virginia. Stored in the Centro Paleobotánico, IMGEMA-Jardín Botánico de Córdoba under locality number 8779.

*Neotype* – The specimen figured on Plate 4, figure 1.

*Description* – Frond at least bipinnate (frond size unknown). Rachis of the penultimate order up to 12 mm wide (in the lower part of penultimate pinna on Pl. 2). Last order pinnae gradually tapering in the terminal part and showing a small, rounded apical pinnule. Ultimate rachises sturdy, up to 2 mm wide. Lateral pinnules showing bilateral symmetry and a sub-perpendicular position on the rachis. Pinnules slightly constricted just above the base; no perceptible confluence. Length/breadth ratio of pinnules about 3.0-3.25 (dimensions 0.6-1.3 mm length and 0.2-0.4 mm breadth); pinnules parallel-sided to very slightly convex, with rounded apices. Midrib strongly marked, straight, extending to near the pinnule apex; lateral veins perpendicular to both the midrib and the pinnule margin, usually once forked near the midrib and relatively crowded (34-40 veins per cm on the pinnule margin).

*Remarks* – The above description refers to Fontaine & White's specimens (1880, pl. 33, figs 2, 3; Pl. 2 herein), as well as to the more fragmentary remains from the type area (Pl. 4; Pl. 5, figs. 1, 2). It replaces the original description by Fontaine & White (1880) which is quoted as follows: "Frond tripinnate; primary rachis strong and rough; primary pinnae triangular in outline, and tapering rapidly to the summit; secondary pinnae, opposite or alternate, going off at nearly a right angle, long and tapering slowly, with a large and rather rigid rachis; pinnules, alternate, separate below but united above, and becoming more so as we approach the summit of the primary pinnae where

the pinnules have all united, and the ultimate pinnae are reduced to long, undulate or lobed pinnules, which finally pass into simple pinnules of the normal kind; the pinnules also coalesce towards the ends of the ultimate pinnae and are often swollen at the base, as if by two sori, placed one on each side of the mid-nerve at the base, as shown in fig. 1, Pl. XXXIII [= Pl. 2, fig. 1 herein]; mid-nerve well marked, and extending to the apex; lateral nerves numerous, closely placed, going off nearly at right angles with the mid-nerve. Very fine, forking once normally, or with one of the branches, (occasionally both) again forking, simple nerves occasionally interspersed, all proceeding nearly parallel to each other to the margin; lowest pinnule on each side of the base of the pinna, of the ultimate order, heteromorphous by having the lower side of the pinnule lobed while the upper side is entire."

Fontaine & White remarked upon "two sori, placed one on each side of the mid-nerve" as illustrated in the drawing of three pinnules figured as their (1880, pl. 33, fig. 1). It is difficult to know what is meant in this case. Sori are out of the question.

Fontaine & White (1880, pl. 33, fig. 2; Pl. 2 herein) shows an extremely wide rachis in what appears to be the lower part of a penultimate pinna with pinnules in the lower part of last order pinnae showing incipient lobing. If their figures 2 and 3 are regarded as typical, their figure 4 is apparently different since it shows confluent pinnule bases and an almost subtriangular pinnule shape. However, their figure 4a shows an apparently constricted pinnule base, which is contradictory. This tends to suggest inaccuracy in drawing.

The specimens collected from the Cassville Shale by R.H.W. are all quite fragmentary remains of last order pinnae. Equally small are the pinnae fragments illustrated by Gillespie *et al.* (1975), Cross *et al.* (1996) and Blake *et al.* (2002), but the venation seems better preserved in the specimens figured here (Pl. 4, fig. 1; Pl. 5, figs. 1, 2).

*Comparisons* – *Callipteridium costei* is closely similar (Pl. 3), with particular regard to pinnule shape and insertion, even to the extent where the strongly vaulted pinnule bases appear to lack the narrow confluence between pinnules. The pinna terminals are also quite comparable. The only apparent difference is in the slightly curved lateral veins which seem to be once to twice forked in *C. costei* and which show a lower vein density (28-36 veins/cm, according to Knight, 1983). Although a wider variation in pinnule length has been recorded for *C. costei* (up to 20 mm length at 4 mm wide), the average dimensions of pinnules in both species are quite similar. Strongly reduced intercalary pinnae have been observed for *C. costei* by Laveine *et al.* (1977, pl. 10, figs. 2, 2a), but intercalary pinnules are lacking. It thus conforms to the subgenus *Praecallipteridium*.

The differences with *Callipteridium virginianum* are slight, but the two taxa should be kept separate, at least for the time being.

*Discussion* – Gillespie & Pfefferkorn (1986) synonymised *Alethopteris leonensis*, from the Stephanian of northwest Spain, with *Alethopteris virginiana*, as represented by the form redescribed here as *C. virginianum*. Although this synonymy was accepted provisionally by Wagner (1983, pp. 73, 80) and also, with reservations, by Castro (2005b, p. 56), it is now realised that this acceptance was premature. In fact, Wagner's species is a true *Alethopteris*, with decurrent pinnule bases, whilst Fontaine & White's species shows pinnules with a bilateral symmetry, which is characteristic of *Callipteridium*. Indeed, the

American species is most similar to *C. costei*. This is a unusual, but widely distributed species (see Knight, 1983, for an exhaustive discussion).

*Callipteridium virginianum* is here restricted to the specimens figured on Fontaine & White's (pl. 33) and, possibly, the small fragments depicted on their (pl. 32, figs. 3, 5). The new description therefore amounts to a species emendation, since most of the specimens figured as *A. virginiana* by Fontaine & White's are excluded.

More problematical is the specimen figured as *A. virginiana* on Fontaine & White's (pl. 33, figs. 4, 4a). This specimen is shown with confluent pinnule bases in figure 4, but with a constricted pinnule base in figure 4a. It is here assumed that the larger drawing (fig. 4) is inaccurate.

*Occurrence* – North America, Waynesburg Coal, lower Dunkard of West Virginia.

*Stratigraphic range* – Stephanian C?

## Genus *Alethopteris* Sternberg, 1825 emend. Zodrow & Cleal, 1998

*Type species* – *Alethopteris lonchitica* Schlotheim, 1820, *ex* Sternberg, 1825.

### *Alethopteris leonensis* Wagner, 1964
Fig. 2B; Pl. 5, fig. 3; Pls. 6-9; Pl. 10, figs. 1-3; Pl. 11.

v      1959b *Alethopteris leonensis* Wagner, pp. 410, 413 [*nomen nudum*].
v      1962b *Alethopteris leonensis* Wagner, pp. 2394-2395 [*nomen nudum*].
v      1963 *Alethopteris leonensis* Wagner, pp. 91, 95, 96, 97, 99 [*nomen nudum*].
       1963 *Alethopteris leonensis* Wagner; Álvarez-Ramis, p. 71, pl. 2, fig. 3 [*nomen nudum*].
* v    1964 *Alethopteris leonensis* Wagner; Wagner, pp. 841, 842, 843, 846, pl. 2, fig. 20.
v      1965a *Alethopteris leonensis*, Wagner; Wagner, pp. 49-53, pl. 26, figs. 69-72a, pl. 27, fig. 71a, text-fig. 13.
* v    1965b *Alethopteris leonensis* Wagner; Wagner, pp. 50, 51, 54, 57, 58, 69, 79, pl. 47, fig. 96 [= Wagner, 1964, pl. 2, fig. 20]; pl. 48, fig. 97 [= Wagner, 1965a, pl. 26, fig. 69].
* v p1968 *Alethopteris leonensis* Wagner; Wagner, 85-89, pl. 28, figs. 80, 80a, figs. 81, 81a [= Wagner, 1964, pl. 2, fig. 20], pl. 29, fig. 82 [= Wagner, 1965a, pl. 26, fig. 69], pl. 29, figs. 83-83a; *non* pl. 29, figs. 84, 84a [= *Alethopteris lesquereuxii* Wagner, 1968].
v      1970 *Alethopteris leonensis* Wagner; Wagner & Artieda, pl. 4, fig. A.
       1970 *Alethopteris leonensis* Wagner; Doubinger, pp. 279, 281, pl. 16, fig. 3.
v      1971 *Alethopteris leonensis* Wagner; Knight, pp. 218, 219, 220, pl. 3, fig. 1.
v      1974 *Alethopteris leonensis* Wagner; Knight, pp. 289, 290, 293, 294, 295, 296, 297, 298, 300, 302, pl. 3, fig. 4.
v      1983 *Alethopteris leonensis* Wagner; Knight, pp. 210-211, pl. 10, figs. 1, 1a, fig. 2 [= Knight, 1971, pl. 3, fig. 1], fig. 3 [= Knight, 1974, pl. 3, fig. 4].
v      1983 *Alethopteris leonensis* (= *Alethopteris virginiana* Fontaine & White?); Wagner, pp. 165, 166, 167.
v      1985 *Alethopteris leonensis* Wagner; Wagner, p. 202, pl. 2, fig. 3 [mentioned as = *Alethopteris virginiana*].
v      2005a *Alethopteris* cf. *virginiana* Fontaine & White; Castro, pp. 76, 86.
v      2005b *Alethopteris* cf. *virginiana* Fontaine & White; Castro, pp. 56, 57, pl. 27, figs. 1, 2.

*Material and repository* – A total of more than 300 specimens, practically all fragments of pinnae of the last order, mainly from the Ciñera-Matallana (90) and Villablino (192) coalfields in northern León. Apart from the types and additional specimens figured in Wagner (1964, 1965a, 1968), which were deposited in the collection of the

Geologisch Bureau, Heerlen (presently in the NCB Naturalis in Leiden), all specimens including those figured in the present paper are stored in the Centro Paleobotánico, IMGEMA-Jardín Botánico de Córdoba.

*Description* – (After Wagner, 1968, with modifications.) Frond probably at least tripinnate. Rachis of penultimate order rather stout (up to 4 mm wide), with fine longitudinal striae. Pinnae of the last order gradually tapering; terminal small and parallel-sided. Rachis of the last order moderately strong (0.5-1.0 mm wide). Pinnules distant and narrowly confluent, becoming more pecopteroid in the lower parts of pinnae. Insertion of the pinnules varies from slightly oblique to perpendicular, depending on the position in the frond. Pinnules generally rather long and slender (usually about 11 mm long and 3 mm broad), with parallel or subparallel margins and a bluntly acuminate apex; tending towards a more nearly subtriangular shape where shorter pinnules are found, that is, near the top parts of pinnae. Pinnule lamina fairly thick, vaulted; a compression border is sometimes developed. Midrib strongly marked, straight, and deeply immersed in the pinnule lamina. Lateral veins relatively well-marked, rather coarse and following an almost straight course from the midrib to the pinnule margin which is reached at approximate right angles; usually once, less commonly twice forked at fairly irregular intervals, although mainly near the midrib. Vein density ranging from 44 to 50 veins per cm on the pinnule margin. Associated 'seeds' with coarse ribbing (*Holcospermum*).

*Comparisons* – This species is most closely similar to *Alethopteris bohemica*, another Stephanian species with a similar stratigraphic range (Cantabrian to Stephanian C for *Alethopteris bohemica* and upper Barruelian to Stephanian C for *Alethopteris leonensis*). However, *A. bohemica* shows even more generalised pecopteroid pinnules with a different length-breadth ratio, being relatively broader. Its venation is marginally more crowded (*c.* 55 veins/cm), although this might be interpreted as being due to a relatively greater width of the pinnules. Where only fragmentary specimens are available, the two species may be confused because a certain amount of morphological overlap is apparent. The associated 'seeds' are quite similar though more finely ribbed in *A. bohemica* (*Rhabdocarpus*; see Pl. 12, fig. 3). Apart from those documented by Wagner (1965a,b, 1968) and Castro (2005a,b), three specimens of *A. bohemica* from the Saberian of La Magdalena (León) and another from the Stephanian B of Villablino are figured in the present paper (Pl. 10, fig. 4; Pl. 12, figs. 1, 2, 4), so as to provide immediate comparison. *Alethopteris bohemica* is a European species which has also been recorded from North America (Blake *et al.*, 2002), including the lower Dunkard (albeit doubtfully). A recent illustration from the Cañon del Cobre Formation in New Mexico (DiMichele *et al.*, 2010), as *Alethopteris zeilleri* Ragot ex Wagner, 1968, apparently represents *A. bohemica*.

Another comparable species, *Alethopteris lesquereuxii* Wagner, 1968, is characterised also by fairly elongate pinnules which, however, show more tapering margins. On the whole, the pinnules of *A. lesquereuxii* are more markedly confluent than those of *A. leonensis*. The vein density is also different, that is, 30-35 veins/cm in *A. lesquereuxii*, as against 44-50 veins/cm in *A. leonensis*. The original description of *A. lesquereuxii* (Wagner, 1968) was based on a number of pinna fragments from the upper Asturian and

lower Cantabrian strata of the Guardo Coalfield in the Cantabrian Mountains of north-west Spain (see also the illustrations in Wagner, 1983), as well as material from strata of similar age at Cannelton, Pennsylvania (U.S.A.), and from South Wales (at the same stratigraphic level, Grovesend beds). This species has also been identified from strata of similar age in the Sydney Basin of Nova Scotia (see further comments below) and from the Mazon Creek flora in Illinois, U.S.A. (Wittry, 2006). A distinction was made in 1968 between the type variety and *A. lesquereuxii* var. *cerverae* Wagner, which is here incorporated in the intraspecific variability of *A. lesquereuxii*. Moreover, usage of this species over the past forty years has shown that *Alethopteris kanisii* Wagner, 1968, another species described from the same beds in the Guardo Coalfield (where *A. lesquereuxii* is reasonably common), should probably be incorporated with the latter (as mentioned also by Wagner, 1983, p. 85). *Alethopteris kanisii* was described from quite fragmentary remains representing slightly broader pinnules than those characterising *A. lesquereuxii*. Also, the pinna terminal figured for *A. kanisii* is broader than is customary for *A. lesquereuxii*. The types of *A. kanisii* are probably insufficient for a proper characterisation of this species which should be allowed to lapse.

Zodrow & Cleal (1998) postulated that *A. lesquereuxii* might be a synonym of *Alethopteris ambigua* Lesquereux, 1879. These two species are certainly similar and some morphological overlap may exist. They also occur in beds of the same age (mainly late Asturian). However, the pinnules of *A. ambigua* (a synonym of *Alethopteris lonchitica*, see Wagner & Álvarez-Vázquez, 2008) are generally smaller and more parallel-sided, and its pinnae show a smaller apical pinnule than seems to be customary for *A. lesquereuxii*. Although the pattern is similar in both species, *A. lesquereuxii* tends to have a slightly more crowded venation. A wide midrib is characteristic of the underside of *A. ambigua* pinnules which, on the whole, are more vaulted than those of *A. lesquereuxii*. A certain amount of confusion is possible. Indeed, Zodrow & Cleal (1998) figured as *A. ambigua* specimens from the Sydney Coalfield in Nova Scotia, which they had named previously *A. lesquereuxii*, an identification which should probably have been maintained. Similar remains from the same area (Sydney Basin in Nova Scotia) were figured previously by Wagner (1968) as *A. ambigua* var. *gibsonii* Lesquereux (see comments in Wagner & Álvarez-Vázquez, 2008, p. 164). The latter identification now seems questionable, because *Alethopteris gibsonii* as introduced by Lesquereux (1879-80) cannot very well be judged from the diagrammatic drawings as published.

Zodrow & Cleal (1998, p. 97) suggested that *A. leonensis* might be a descendant of *A. ambigua* (that is, *A. lesquereuxii*). However, the published ranges of *A. lesquereuxii* and *A. leonensis* leave a gap in time corresponding to the lower Barruelian.

*Alethopteris moravica* Augusta, 1927, as figured and redescribed by Wagner (1967) and Šimůnek (1989), is another comparable species. However, it exhibits more biconvex pinnules with a more markedly confluent base and a denser venation (55-65 veins/cm, according to Šimůnek, 1989). Its vein pattern is also different, with more curved lateral veins. *Alethopteris moravica* is only known thus far from its type locality, Seam I of the Rosice-Oslavany Formation in the Boskovice Basin, Moravia (Stephanian C age).

The two specimens illustrated by Elias (*in* Moore *et al.*, 1936, fig. 6.89) as *Alethopteris kansasensis* Elias from the 'Lower Permian' of Kansas, U.S.A., seem quite comparable to *A. leonensis* and might well represent the same species. Elias did not provide a diagnosis of *A. kansasensis* which is regarded as an invalid or illegitimate species (Wagner, 1968,

p. 87; Winston, 1983, p. 7). Elias referred to it as belonging to the *Alethopteris lonchitica* group and there is, indeed, a resemblance with *A. lonchitica* (which is the proper name for *A. ambigua*). It is noted that the venation diagram published by Elias (*in* Moore *et al.*, 1936, fig. 8, ill. 5) shows *c*. 30 veins/cm which suggests *A. lonchitica* rather than *A. leonensis*.

*Remarks on synonymy* – As follows from the list of synonymy, *A. leonensis* has been recorded mainly from the Iberian Peninsula. However, there is also a record from the Mont Pelé Formation (Stephanian B) of the Autun Basin in south central France (Doubinger, 1970). Although the venation is hardly visible on Doubinger's illustration at natural size, the pinnule size, shape and insertion conform to typical *A. leonensis*. There seem to be no additional records of this species from the Massif Central (France). A single specimen illustrated as *A. virginiana* from the lower Dunkard in the Appalachian area of North America (Blake *et al.*, 2002, pl. 7, fig. 3) resembles *A. leonensis*. However, near terminal fragments of *Callipteridium costei* as figured by Zeiller (1906) are also alethopteroid. The small fragments figured from the Alps by Vinassa de Regny *in* Vinassa de Regny & Gortani (1905, p. 483, pl. 12, figs. 10-12) as *A. lonchitica*, and which Wagner (1968) tentatively assigned to *A. leonensis*, are probably insufficient for a reliable identification. Wagner & Álvarez-Vázquez (2008) tentatively compared these illustrations with *A. lonchitica* (= *A. ambigua*). Likewise, it seems that the specimen figured as *Alethopteris serlii* (Brongniart, 1828) Göppert, 1836 by Purkyně (1929, pl. 4, figs. 1, 2), tentatively included with *A. leonensis* by Wagner (1968, p. 88), is better referred to *A. lonchitica* (= *A. ambigua*). This specimen is from the lower Cantabrian of the Plzeň Basin in Bohemia and is a small terminal fragment of a pinna of the last order.

*Remarks on figured specimens* – A full representation of the available pinna fragments shows the shape of terminals and length/breadth ratios of the lateral pinnules. It includes new material from the type area, the Ciñera-Matallana Coalfield (Saberian age) in the province of León. Additional specimens showing the same characteristics are illustrated here for the first time from the Villablino Coalfield (Stephanian B), also in northern León. These correspond to a large collection of pinna fragments with associated 'seed' adpressions, identified as *Holcospermum* (Pl. 8, fig. 2). Three additional pinna fragments from the Saberian of La Magdalena (León) complement the recent illustration from this coalfield by Castro (2005b).

A terminal of the penultimate order (Pl. 8, fig. 3) shows the rapid transition from an average pinnule length (7-9 mm) to lengthened, still entire pinnules (18 mm) passing rapidly to a last order pinna with moderately confluent, short pinnules. The lower part of this specimen displays part of a pinna with well individualised pinnules showing narrowly confluent bases and a subtriangular shape. This specimen from Villablino is quite comparable with *A. leonensis* as figured from Ciñera-Matallana by Wagner (1965a, pl. 26, fig. 69).

The appreciable range in the length of pinnules, whereas their width remains more constant, shows that apical growth was the norm. The longest pinnule figured (Pl. 9, fig. 3), with 23 mm length at 5 mm width, occupies a position in a penultimate pinna fragment where there is a gradual transition to a last order pinna. More ordinary lat-

eral pinnules range from 5 to 12 mm length at 3-5 mm width. Where fully developed pinnules are represented, these are shown to be well spaced, with narrowly confluent bases. The shorter pinnules tend to be subtriangular, whereas the longer ones are more parallel-sided. All the fully developed pinnules show bluntly acuminate apices which are characteristic. Pinna terminals show generally elongate, more or less well individu-alised apical pinnules of similar characteristics to the lateral pinnules. The pinnule lamina is vaulted. A compression border is occasionally present (Pl. 9, fig. 1) depending on the appropriate lithology.

The venation invariably shows a relatively wide, straight midrib extending into the pinnule apex. Lateral veins curve slightly away from the midrib and straighten almost immediately to adopt a nearly perpendicular position onto the pinnule margin. Apart from an occasional bifurcation near the midrib, the lateral veins generally fork once at irregular distances from the midrib (see Pl. 7, fig. 4; Pl. 11, fig. 2).

*Occurrence* – Spain: Sabero, Ciñera-Matallana, La Magdalena, Puerto Ventana, Villa-blino, El Bierzo, Tineo, Cangas del Narcea coalfields, all in the Cantabrian Mountains, northwest Spain, and in the Puertollano Basin (province Ciudad Real, south-central Spain). France: Massif Central, Autun Basin (Mont Pelé beds). Although *A. leonensis* is reasonably common, it is not found quite as regularly as the comparable species *A. bohemica*.

*Stratigraphic range* – Upper Barruelian (Sabero), Saberian (Sabero, Ciñera-Matallana, La Magdalena, Puerto Ventana), Stephanian B (Villablino, El Bierzo, Tineo, Cangas del Narcea, Autun), Stephanian C (Puertollano).

## Conclusions

A reinterpretation of taxa figured and described by Fontaine & White (1880) suggests that Autunian assemblages are represented (probably lower Autunian = Stephanian C for the basal Dunkard). A proper reevaluation of the Dunkard flora needs new collections of similar quality to that available in the late 19th Century. Fontaine & White's *Alethopteris virginiana* is restricted to the form redescribed here as *Callipteridium (Praecallipteridium) virginianum* (Fontaine & White) comb. nov. Although previously regarded as identical with the Spanish taxon *Alethopteris leonensis*, this is no longer considered as correct. *Alethopteris leonensis* ranges from upper Barruelian to Stephanian C. *Callipteridium virgin-ianum* seems later (Stephanian C = lower Autunian).

## Acknowledgements

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**Plate 1**

Fig. 1. cf. *Polymorphopteris subelegans* (Potonié) Wagner. After Fontaine & White (1880, pl. 32, figs 1, 1a) as *Alethopteris virginiana*. Specimen lost. Basal Dunkard (Upper Pennsylvanian).
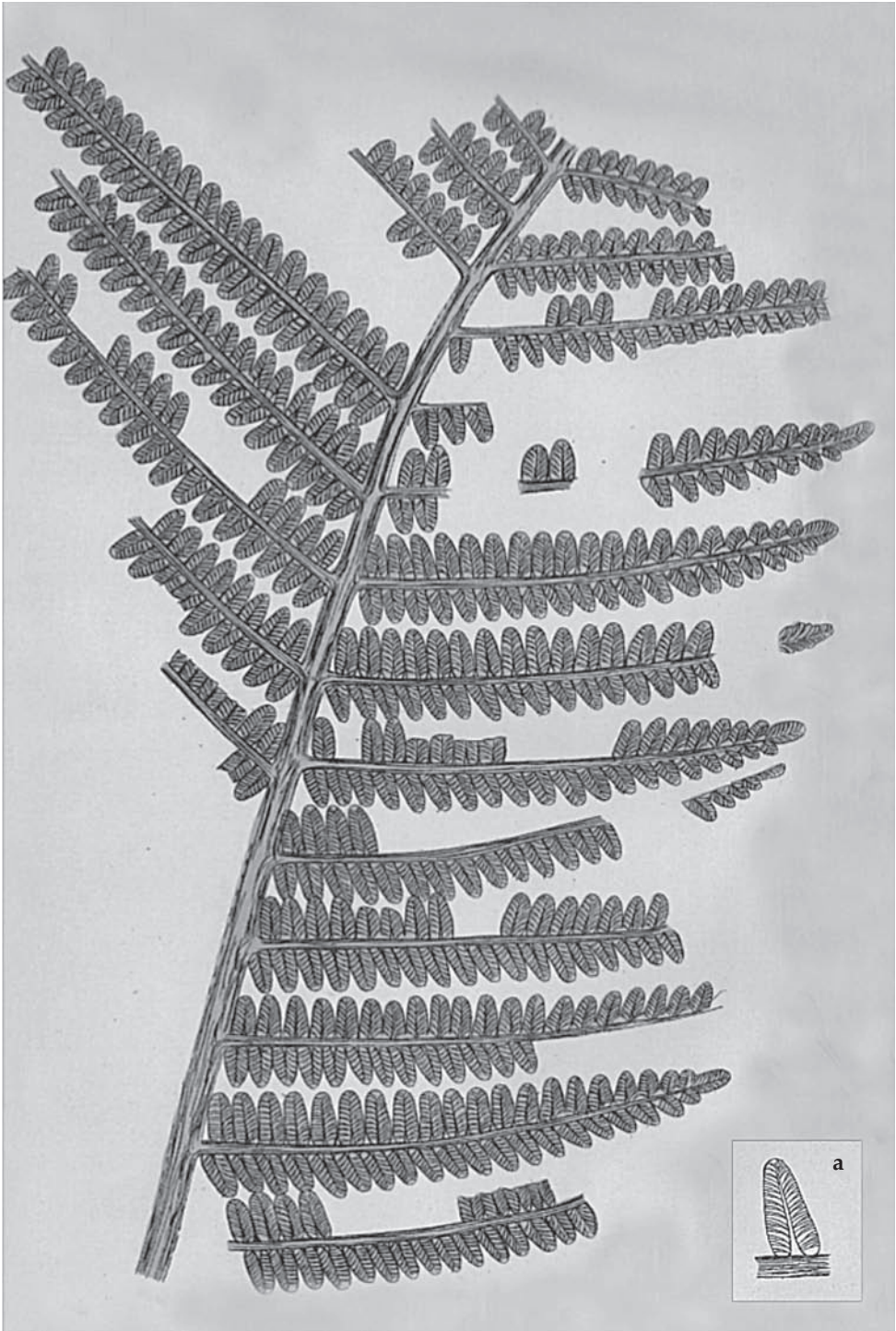
**Plate 2**

Figs. 1, 2. *Callipteridium virginianum* (Fontaine & White) comb. nov. Copy of Fontaine & White (1880, pl. 33, figs. 1, 2) as *Alethopteris virginiana*. Specimen lost. Basal Dunkard (Upper Pennsylvanian).
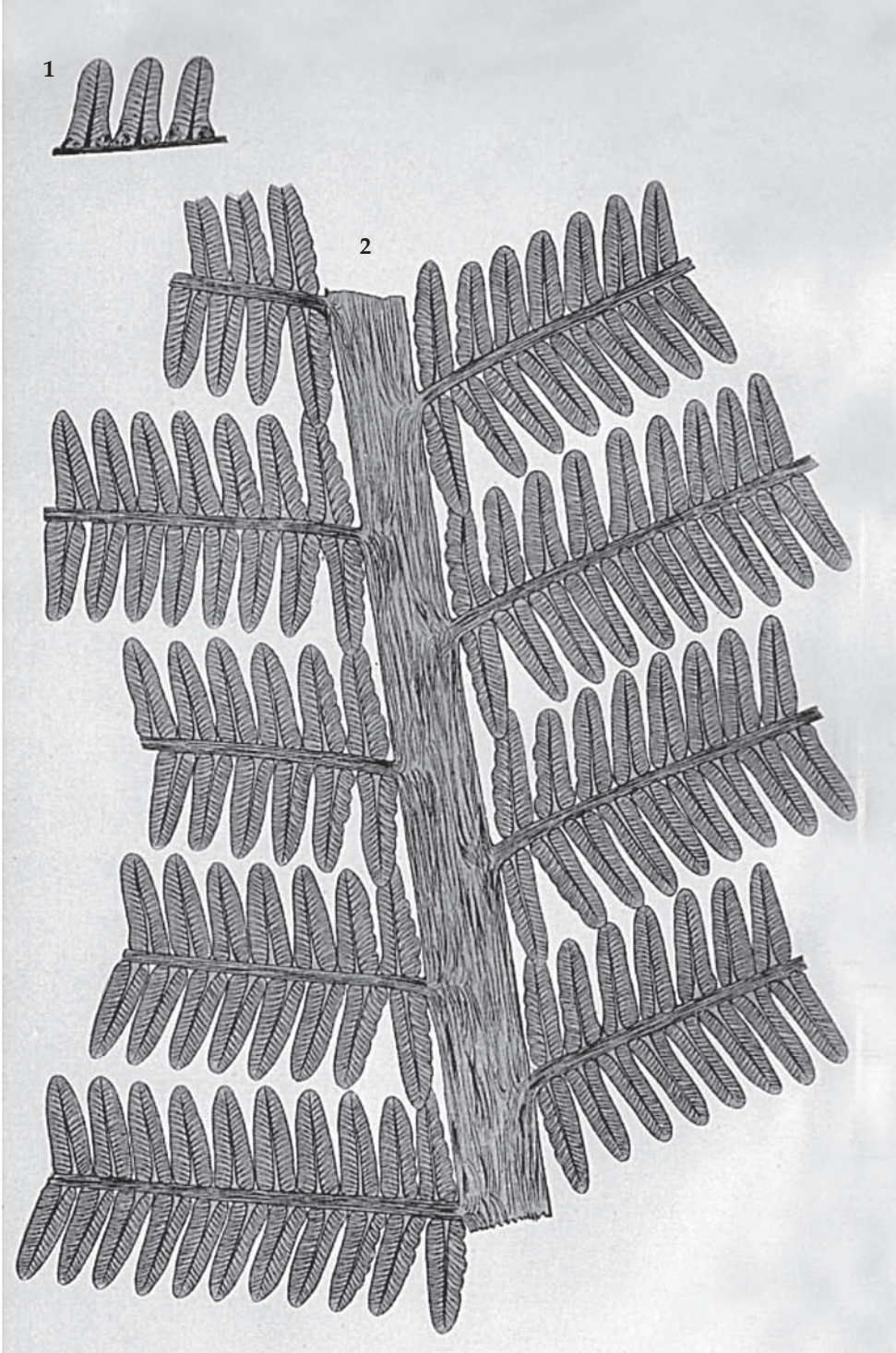
**Plate 3**

Fig. 1. *Callipteridium costei* (Zeiller) Wagner. Partial copy of Zeiller (1906, pl. 15, figs. 1, a, b) as *Alethopteris costei*. Type specimen. Découverte Sainte-Hélène, Blanzy Coalfield, Montceau Beds, Massif Central (France). Stephanian C.

**Plate 4**

Figs. 1, 2. *Callipteridium virginianum* (Fontaine & White) comb. nov. Locality 8779: road bend near Cass-ville, West Virginia, U.S.A., shale parting in upper part of the Waynesburg coal, basal Dunkard beds. Collected with W.H. Gillespie in 1995. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.

Fig. 1. Part of a last order pinna (× 6), showing the perpendicular insertion of pinnules with a slight con-striction above the base; also the strongly marked midrib and crowded, once forked, straight, lateral veins, abutting perpendicularly onto the pinnule margin. Neotype.

Fig. 2. Part of last order pinna (× 3) with perpendicularly inserted lateral pinnules.

**Plate 5**

Figs. 1, 2. *Callipteridium virginianum* (Fontaine & White) comb. nov., from Cassville, West Virginia, U.S.A. Collected with W.H. Gillespie in 1995. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.

Fig. 1. Detail of several pinnules (× 5), showing the constriction above the base and the strongly marked midrib. Locality 8779 (Cassville Shale). Basal Dunkard.

Fig. 2. Fragment of last order pinna (× 4) with pecopteroid, parallel-sided lateral pinnules, with rounded apices. Note the bilateral symmetry characteristic of *Callipteridium*.

Fig. 3. *Alethopteris leonensis* Wagner. Enlargement (× 5) of the specimen in (Pl. 7, fig. 3). Locality 10325 (Calderón beds, Villablino Coalfield), Cantabrian Mountains, northwest Spain. Stephanian B. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.
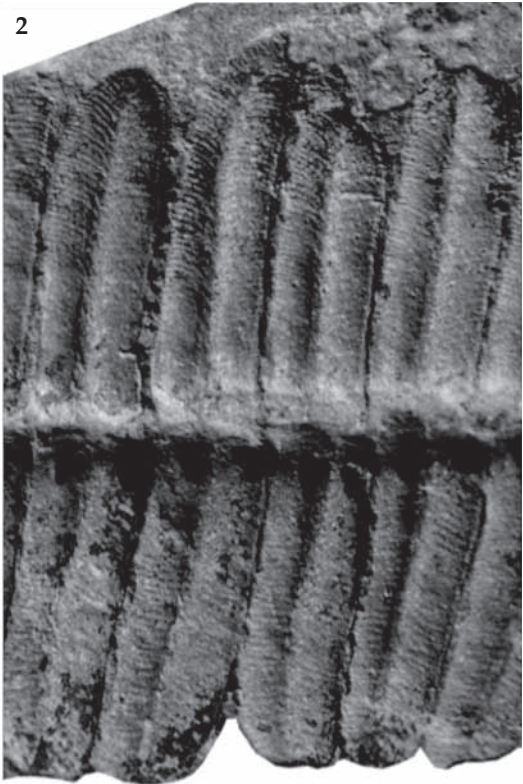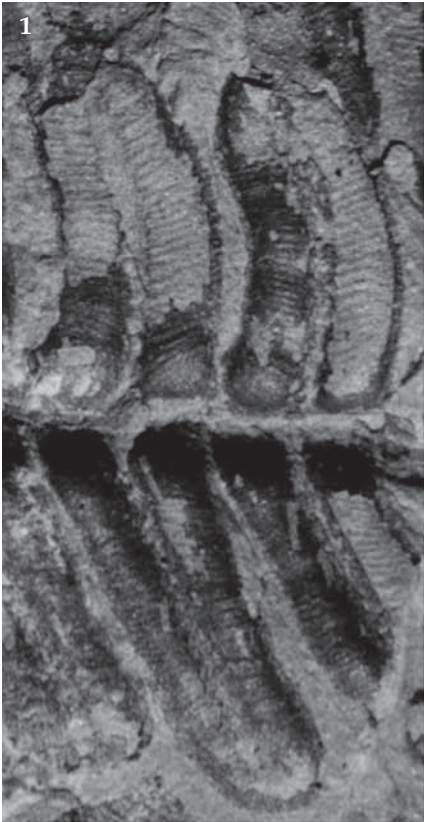
**Plate 6**

Figs. 1-3. *Alethopteris leonensis* Wagner. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.

Fig. 1. Terminal part of a pinna of the last order (× 3) showing ribbon-shaped apical pinnule and well-spaced lateral pinnules with confluent bases. Locality 10325 (Calderón beds, Villablino Coalfield). Stephanian B.

Fig. 2. Terminal part of a pinna of the last order (× 3). Locality 2500 (San José Formation, Ciñera-Matallana Coalfield). Saberian.

Fig. 3. Medial part of a pinna of the penultimate order (× 3) showing average-sized pinnules, well-spaced, with confluent bases. Locality 1075 (San José Formation, Ciñera-Matallana Coalfield). Saberian.
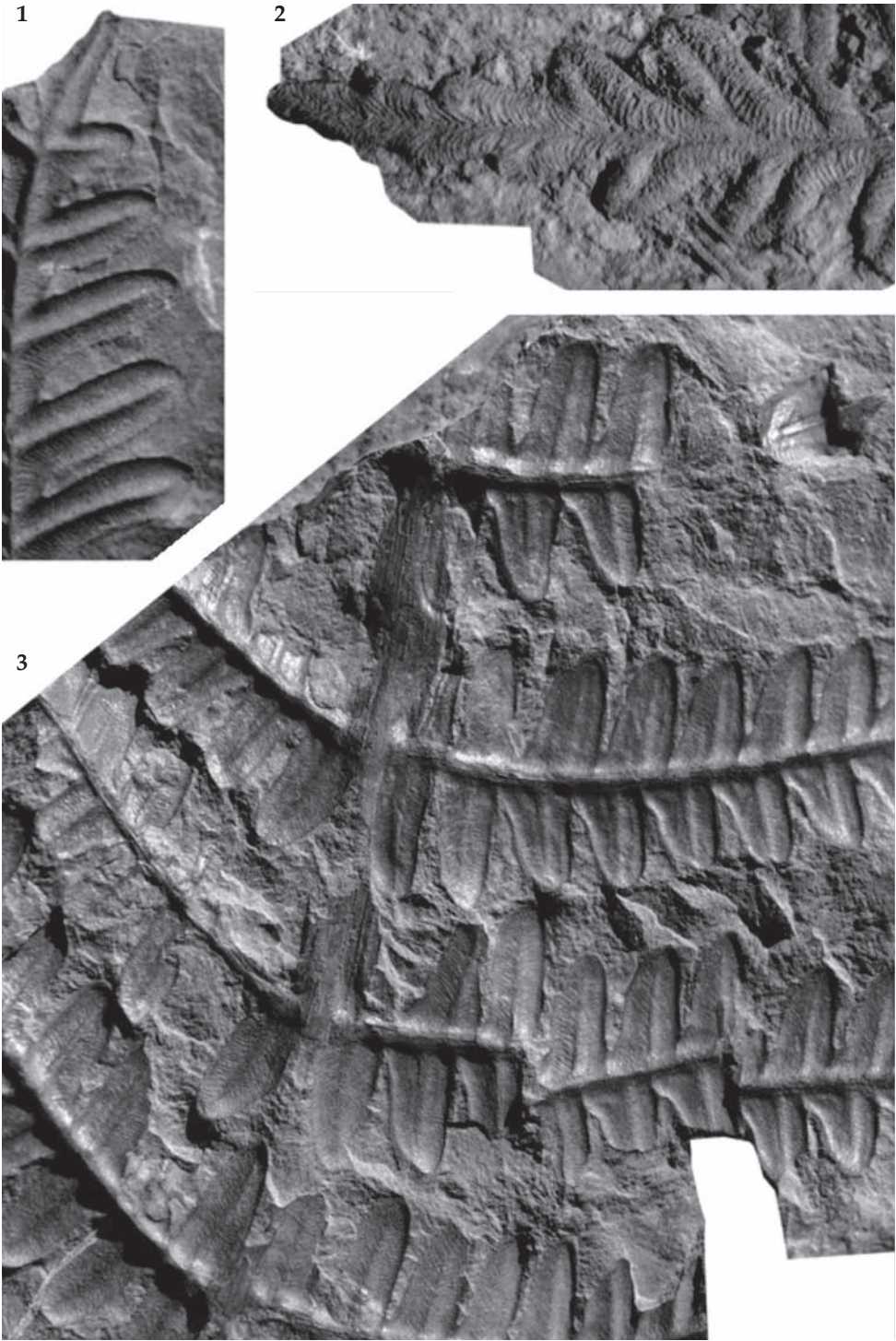
**Plate 7**

Figs. 1-4. *Alethopteris leonensis* Wagner. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.

Fig. 1. Pinna of the last order (× 3) with gradually fused terminal; apical pinnule poorly developed. Note narrowly confluent pinnule bases. Locality 1337 (Vulcano Seam = Seam 1, San José Formation, Fuentescala Valley, Ciñera-Matallana Coalfield). Saberian.

Fig. 2. Sub-perpendicularly inserted pinnules (× 4) with narrowly confluent bases and subtriangular shape. Locality 1337 (Vulcano Seam = Seam 1, San José Formation, Fuentescala Valley, Ciñera-Matallana Coalfield). Saberian.

Fig. 3. Part of last order pinna (× 3) with more elongate pinnules showing sub-acuminate apices. Locality 10325 (Calderón beds, Villablino Coalfield). Stephanian B.

Fig. 4. Two pinnules (× 5) showing the strongly marked midrib and once forked laterals; vein bifurcations at variable distances from the midrib. Locality 2500 (San José Formation, Ciñera-Matallana Coalfield). Saberian.
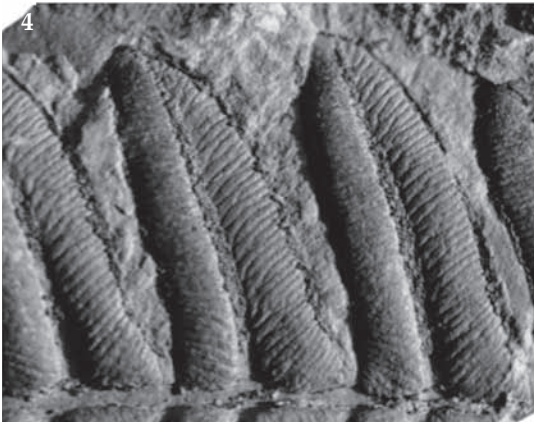
**Plate 8**

Figs. 1, 3. *Alethopteris leonensis* Wagner. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.

Fig. 1. Penultimate pinna fragment (× 3) showing terminals as well as the well-spaced lateral pinnules, confluent at the base. Locality 10325 (Calderón beds, Villablino Coalfield). Stephanian B.

Fig. 3. Terminal part of a pinna of the penultimate order (× 3) showing the rapid transition to last order pinnae, which allows the assumption that a tripinnate element is represented (wide apical angle). Locality 10325 (Calderón beds, Villablino Coalfield). Stephanian B.

Fig. 2. 'Seed' impression (*Holcospermum*) (× 1) found associated with abundant *Alethopteris leonensis* remains. Locality 10325 (Calderón beds, Villablino Coalfield). Stephanian B. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.
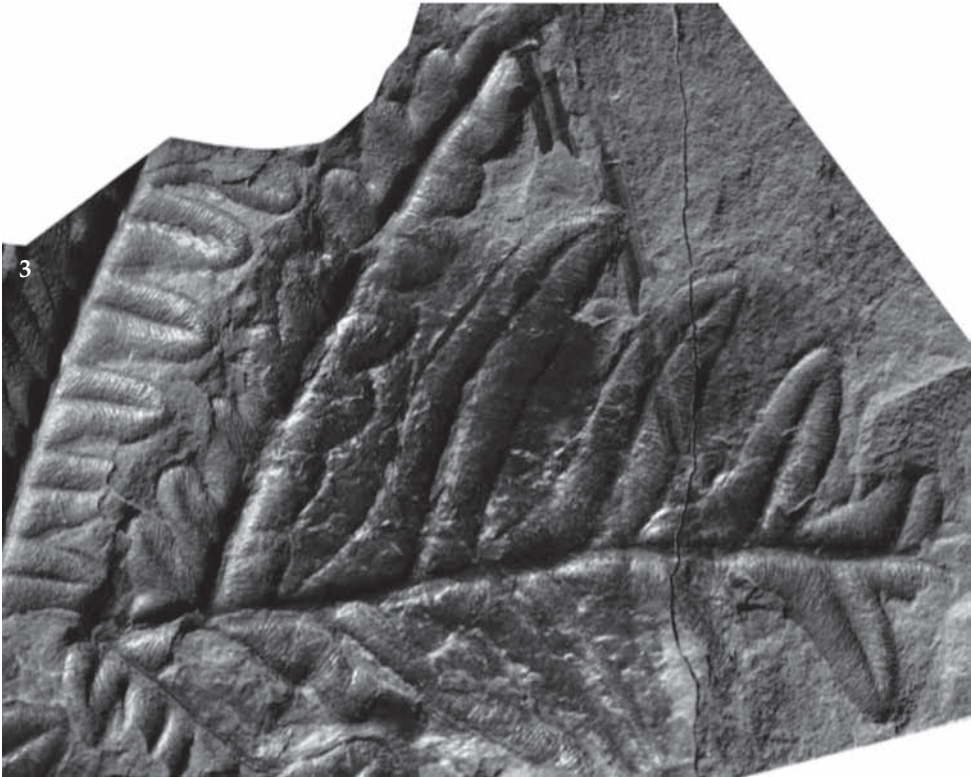
**Plate 9**

Figs. 1-3. *Alethopteris leonensis* Wagner. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.

Fig. 1. Terminal part of last order pinna (× 3) with sub-triangular pinnules partially immersed in the rock. Note compression border. Locality 9995 (near Otero de las Dueñas, La Magdalena Coalfield, higher part of the succession). Saberian.

Fig. 2. Terminal part of last order pinna (× 3). Locality 10325 (Calderón beds, Villablino Coalfield). Stephanian B.

Fig. 3. Fragment of a pinna of the penultimate order (× 3) showing a gradual transition from a lengthened pinnule to the last order pinnae with weakly developed lateral pinnules. This is a bipinnate element. Locality 10325 (Calderón beds, Villablino Coalfield). Stephanian B.

**Plate 10**

Figs. 1-3. *Alethopteris leonensis* Wagner. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.

Fig. 1. Terminal part of a last order pinna (× 2). Locality 10311 (Calderón beds, Villablino Coalfield). Stephanian B.

Fig. 2. Enlargement (× 5) of several pinnules of Figure 1, showing the slightly oblique positioning of asymmetrical pinnules with narrowly confluent bases. Locality 10311 (Calderón beds, Villablino Coalfield). Stephanian B.

Fig. 3. Terminal part of a last order pinna (× 3) showing gradual fusion towards a relatively elongate apical pinnule. Locality 10325 (Calderón beds, Villablino Coalfield). Stephanian B.

Fig. 4. *Alethopteris bohemica* Franke (× 3) showing the rather broad, almost pecopteroid pinnules with sub-acuminate apices, a well marked midrib and crowded, relatively thin, lateral veins. Locality 10311 (Calderón beds, Villablino Coalfield). Stephanian B. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.
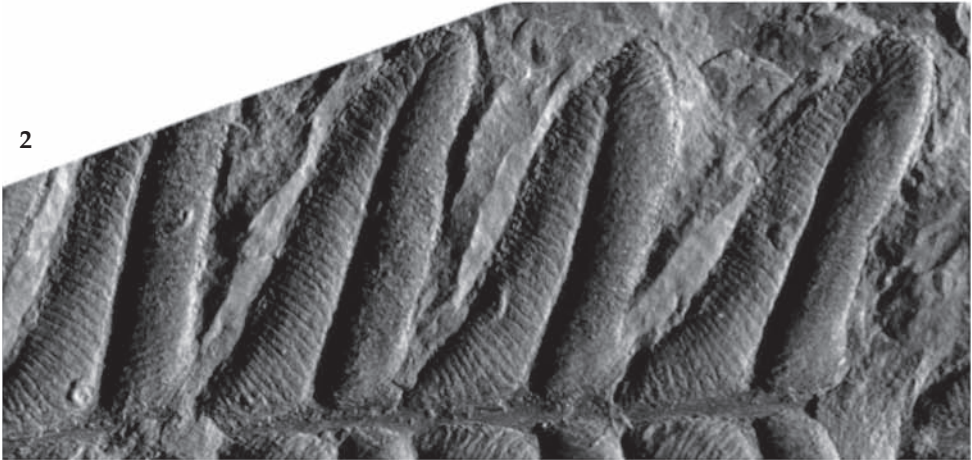
**Plate 11**

Figs. 1, 2. *Alethopteris leonensis* Wagner. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.

Fig. 1. Terminal part of last order pinna (× 5), showing a relatively short, apical pinnule and relatively narrow lateral pinnules with a rapid increase in length. Probably the terminal part of a bipinnate element. Locality 10325 (Calderón beds, Villablino Coalfield). Stephanian B.

Fig. 2. Enlargement (× 9) of two pinnules of the specimen (Pl. 10, fig. 1). Note straight, well marked midrib and thin lateral veins, which are once forked at variable distances from the midrib. Locality 10311 (Calderón beds, Villablino Coalfield). Stephanian B.

**Plate 12**

Figs. 1-4. *Alethopteris bohemica* Franke. Repository: Centro Paleobotánico, Jardín Botánico de Córdoba, Spain.

Fig. 1. Terminal part of last order pinna (× 3) showing the relatively broad pinnules with strongly marked midrib and thin, crowded, lateral veins. Locality 9883 (La Magdalena Coalfield, Irene seam group). Saberian.

Fig. 2. Terminal (× 3) showing gradual fusion of pinnules towards a short, sub-acuminate apical element. Locality 9883 (La Magdalena Coalfield, Irene seam group). Saberian.

Fig. 3. Associated 'seed' (*Rhabdocarpus*) (× 1) found associated with *Alethopteris bohemica*. Locality 9883 (La Magdalena Coalfield, Irene seam group). Saberian.

Fig. 4. Well preserved pinnule (× 3) showing the strongly marked midrib and thin, rather crowded lateral veins, abutting at right angles on the pinnule margin. Locality 9883 (La Magdalena Coalfield, Irene seam group). Saberian.