A REVISION OF THE LOWER PENNSYLVANIAN
Alethopteris lonchitica (auctor) AND ITS IDENTITY WITH
Alethopteris urophylla

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ABSTRACT

One of the most common lower Pennsylvanian (upper Namurian, lower Westphalian) pteridosperms is a species commonly recorded as Alethopteris lonchitica Schlotheim, 1820 ex Sternberg, 1825. However, the photographic illustration of the lectotype of Alethopteris lonchitica by Zodrow & Cleal (1998) has allowed a clear distinction from Alethopteris lonchitica (auctor) which corresponds, in the main, to Alethopteris urophylla (Brongniart, 1834) Göppert, 1836. This species is redescribed here, and its holotype is illustrated photographically for the first time. The published records, backed up by illustration, are analysed with reference to lists of synonymy. The geographic and stratigraphic distribution of Alethopteris urophylla is discussed, and illustrations of this species are provided from Nova Scotia, Scotland, England, Wales, the North of France, and NW as well as SW Spain. Alethopteris lonchitica was identified with Alethopteris lonchitifolia Bertrand, 1932 by Zodrow and Cleal, but the present writers prefer an identification with Alethopteris friedeli Bertrand, 1932. The corresponding taxonomic implications are discussed.

Keywords: Systematic palaeobotany, Alethopteris, lower Pennsylvanian, Canada, Scotland, England, Wales, France, Spain.

RESUMEN

Una de las especies de pteridosperma más citadas en el Pensilvánico inferior (Namuriense superior, Westfaliense inferior) es Alethopteris lonchitica Schlotheim ex Sternberg, 1825. Sin embargo, la figuración fotográfica del lectotipo de esta especie en Zodrow & Cleal (1998) ha permitido demostrar que la mayoría de los ejemplares atribuidos a Alethopteris lonchitica (auctor) corresponden, en realidad, a Alethopteris urophylla (Brongniart, 1834) Göppert, 1836. En este trabajo se redescrive e ilustra fotográficamente, por primera vez, el holotipo de Alethopteris urophylla. Todos los registros avalados por ilustraciones se comentan en las listas de sinonimia. Se estudia también la distribución geográfica y estratigráfica de la especie, figurando ejemplares de Alethopteris urophylla procedentes de Nueva Escocia, Escocia, Inglaterra, País de Gales, Norte de Francia, y del NO y SO de España. Finalmente, se discute la identificación, hecha por Zodrow y Cleal, de Alethopteris lonchitica con Alethopteris lonchitifolia con Alethopteris lonchitidis Bertrand, 1932; en este trabajo se defiende la sinonimia con Alethopteris friedeli Bertrand, 1932, y se analizan las implicaciones taxonómicas que esto supone.

Palabras clave: Taxonomía paleobotánica, Alethopteris, Pensilvánico inferior, Canadá, Escocia, Inglaterra, Gales, Francia, España.

INTRODUCTION

Alethopteris lonchitica, a species introduced by Schlotheim (1804, 1820) as Filicites lonchiticus, and referred to as Alethopteris lonchitidis by Sternberg (1825), has been commonly identified with an upper Namurian to lower Westphalian (lower Pennsylvanian) species of widespread occurrence in the Amerosinian Realm, i.e. the palaeoequatorial belt of Carboniferous times.

It has been apparent for some time that this was likely
to be a misidentification since Schlotheim’s specimen came from upper Westphalian strata in the Saar Coalfield in western Germany. Thomas & Cleal (1993a: 115), quoting Wagner (1968: 107), opted for applying the name of *Alethopteris urophylla* to the upper Namurian-lower Westphalian taxon. They also suggested that the real *Alethopteris lonchitica* would be the same as *Alethopteris lonchitifolia*, *Alethopteris ingbertensis* Kessler, 1916, *Alethopteris missouriensis* White, 1899, *Alethopteris densinervosa* Wagner, 1968 and *Alethopteris westphalensis* Wagner, 1968. This identification is rejected in the present paper in favour of another species from Saarland, *Alethopteris friedelii*, a synonym of *Alethopteris ambiguia* Lesquereux, 1879, according to Wagner (1968). Previously, Scheiing & Pfefferkorn (1980) had placed in synonymy *Alethopteris serliii* (Bronniiart, 1828a) Göppert, 1836, *Alethopteris lonchitifolia*, *Alethopteris ingbertensis*, *Alethopteris missouriensis*, *Alethopteris densinervosa* and *Alethopteris westphalensis*, referring all these species to the “*Alethopteris serliii* group”. Most of these species had been grouped already by Wagner (1968: 172) as regional varieties of *Alethopteris lonchitifolia*. The total synonymy proposed by Scheiing & Pfefferkorn (1980) was rejected by Zodrow & Cleal (1998), who excluded *Alethopteris serliii* (in agreement with Wagner, 1968).

Zodrow & Cleal (1998) published photographs of the type specimen of *Alethopteris lonchitica* which had been rediscovered in the collections of the Museum für Naturkunde in Berlin. In agreement with Thomas & Cleal (1993a), they identified this species with *Alethopteris lonchitifolia*, which had also been described from Saarland. However, this identification is debatable, since *Alethopteris lonchitifolia* possesses more biconvex pinnules, with a denser nervation. Schlotheim’s show more parallel-sided, generally narrower pinnules, with a wider venation. This conforms better to the characters of *Alethopteris friedelii*, another taxon described from Saarland. The latter was regarded as a synonym of *Alethopteris ambiguia* by Wagner (1968), who figured a wide range of specimens of this species from different parts of the palaeoequatorial belt (Amerosian Realm) of Pennsylvanian times, from eastern North America to Asia Minor. This included a photographic illustration of the lectotype (figured originally as a drawing by Lesquereux, 1879: pl. XXXI, figs 1, 1a). Of course, identification with *Alethopteris lonchitica* implies that *Alethopteris ambiguia* is a synonym.

The upper Namurian and lower Westphalian specimens which may be referred to as *Alethopteris lonchitica* (auctorum) (non von Schlotheim), are clearly different. Most of the specimens illustrated in the literature are comparable to *Alethopteris urophylla*, and the opportunity is taken here to refigure Bronniart’s type specimen from Merthyr Tydfill in South Wales. Another species which is commonly regarded as identical is *Alethopteris discrepans*, from eastern Canada. New material from this area has recently become available, and is recorded in the present paper. The present writers also take the opportunity to figure comparable specimens from Scotland, England, the North of France, and two different parts of Spain. Good illustrations are already available from Britain (Crookall, 1955), northern France (Buisine, 1961) and western Germany (Josten, 1991).

**GENERAL COMMENTS ON Alethopteris lonchitica AND SIMILAR SPECIES**

The species *Alethopteris lonchitica* was introduced as *Filicites lonchiticus* by Schlotheim (1804, 1820), and illustrated by means of a composite drawing of several different pinna fragments occurring on two different faces of one and the same rock specimen from the upper Westphalian strata in Saar-Lorraine, a coal basin which straddles parts of Germany and France. The correct attribution of this species has always been problematical in view of the diagrammatic nature of Schlotheim’s illustration, and palaeobotanists have usually followed Zeiller (1886: pl. XXXI, figs 1, 1A) who identified it with a magnificent specimen from the lower Westphalian of the North of France. Additional, well preserved specimens from the North of France were published by Corsin (1932) and Buisine (1961), who monographed the alethopterids from this area. Buisine’s exhaustive documentation of *Alethopteris lonchitica* apparently refers to the species figured and described by Zeiller (1886-88). There is a strong resemblance to *Alethopteris urophylla*, a species described from the lower Westphalian of South Wales, and which is commonly attributed to *Alethopteris lonchitica* in the literature. Records in the literature are most commonly under the name of *Alethopteris lonchitica*, even though this has been regarded as a misidentification (Wagner, 1968), a point of view which the photographic illustration of Schlotheim’s type specimen has confirmed (Zodrow & Cleal, 1998). A complex synonymy has been generated. This is analysed later in the present paper.

Earlier authors have generally ignored the type of *Alethopteris lonchitica*, which was reputedly lost, and Wagner (1968: 107) went so far as to suggest that *Alethopteris lonchitica* might have to be abandoned since its characters were difficult to establish from Schlotheim’s diagrammatic drawing. In fact, the many records of specimens identified as *Alethopteris lonchitica* and the comprehensive lists of synonymy in Crookall (1955) and Buisine (1961) suggest that this species name was used for a variety of forms. Even so, Zeiller’s (1886-88) interpretation of *Alethopteris lonchitica* normally prevailed. Its delimitation from other species, e.g. *Alethopteris decurrens* (Artis, 1825) Frech, 1880, has sometimes given rise to doubt. Gothaan (1953) illustrated a wide range of specimens from the Ruhr District under the name of *Alethopteris lonchitica*, including
Figure 1. Copy of original plate of *Pecopteris urophylla* published by Brongniart (1834: pl. 86).
an *Alethopteris lonchitica* forma *serlii*. This is perhaps one of the more extreme cases of a very broad interpretation of *Alethopteris lonchitica* (*auctorum*).

The rediscovery of the type of *Alethopteris lonchitica* in the Schlotheim Collection in the Museum für Naturkunde in Berlin, and its photographic illustration by Zodrow & Cleal (1998) has allowed this species to become better known. These authors rejected the majority of published records of *Alethopteris lonchitica*, and focused on the various forms described from the Saar-Lorraine Coalfield by

Figure 2. Photograph of Brongniart’s type specimen of *Pecopteris urophylla* from Merthyr Tydfill in South Wales, lower Westphalian (x 1). Repository: Palaeontology Unit, British Geological Survey, Keyworth. Photograph: Barry Pigott, Sheffield University.
Bertrand (1932). This is reasonable since Schlotheim’s type specimen reputedly came from Saarland. They concluded that Alethopteris lonchitica would coincide with Alethopteris lonchitifolia. However, this seems an unfortunate choice, because there is a closer resemblance with Alethopteris friedelii, a species which has been placed in synonymy with Alethopteris ambigua by Wagner (1968). Pinnule shape, vein density, the presence of a compression border which relates to the thickness of pinnule lamina, all these characters shown by the type specimen of Alethopteris lonchitica coincide with those of Alethopteris ambigua. Unfortunately, Zodrow & Cleal (1998) changed the meaning of Alethopteris ambigua so as to include specimens from the Sydney Basin in Nova Scotia, which are more properly regarded as belonging to Alethopteris lesquereuxii Wagner, 1968. Indeed, Zodrow & Cleal (1998: 97) stated that where they used the name Alethopteris lesquereuxii in their earlier, biostratigraphical studies, this should now read Alethopteris ambigua. They also suggested that both species should be regarded as identical (or partly identical according to their list of synonymy for Alethopteris ambigua). They further compared with Alethopteris leonensis Wagner, 1964, which they suggested might be a descendant of Alethopteris ambigua. It is recalled that Alethopteris leonensis was placed in synonymy with Alethopteris virginiana Fontaine & White, 1880, by Gillespie & Pfefferkorn (1986), an identification which may be at least partly correct. Unfortunately, the diagrammatic nature of Fontaine & White’s (1880) illustrations of Alethopteris virginiana leaves room for doubt. Since Fontaine and White’s specimens are no longer available (W.H. Gillespie, pers. comm.), these doubts cannot be dispelled by direct observation. Indeed, it is unclear whether the specimens figured on Fontaine & White’s (1880) pl. XXXII really belong to the same species as those illustrated on their pl. XXXIII, figs 1-4a. There is at least one specimen on their pl. XXXII, fig. 2 which almost certainly represents a pecopterid fern, and it may well be that the entire plate (pl. XXXII, figs 1-5) belongs with the pecopterids. Fontaine and White’s nervation diagram (pl. XXXII, fig. 1a) suggests that Polymorphopteris sublegans (Potonié, 1893) Wagner, 1959 may be involved. The Alethopteris virginiana, as meant in Fontaine & White’s description (1880: 88-89), seems to be represented by the specimens figured on their pl. XXXIII, figs 1-4a. One of the present writers (RHW) has had the privilege of being allowed to collect from the shale parting (Cassville Shale) in the Waynesburg Coal, under guidance from W.H. Gillespie. The remains recovered from this locality (Fontaine & White’s type locality) include an Alethopteris which is the same as Alethopteris leonensis. If these remains are identified with Alethopteris virginiana pars, this may be regarded as the senior synonym, although a neotype will have to be designated; a doubtful procedure if Fontaine & White’s concept of their species is to be identified correctly.

The three species, Alethopteris ambigua, Alethopteris lesquereuxii, and Alethopteris leonensis (= Alethopteris virginiana pro parte) are certainly comparable, though probably not identical. It is noted that Zodrow & Cleal (1998) overlooked the illustration of specimens attributed to Alethopteris ambigua var. gibsonii Lesquereux, 1879 from Point Aconi Seam in the Sydney Basin by Wagner (1968: 39-40, pl. 4, figs 15-18a). These specimens were described separately from undoubted Alethopteris ambigua. They are quite comparable to the specimens illustrated from the Hub and Upper Bonar seams by Zodrow & Cleal (1998). Perhaps, the Point Aconi specimens which were attributed to Alethopteris ambigua var. gibsonii by Wagner (1968), should be referred to Alethopteris lesquereuxii. Indeed, their slightly higher vein density would point in this direction. Earlier illustrations under the name of Alethopteris friedelii by Bell (1938), also from the Sydney Coalfield, are shown at natural size and cannot be judged very well from the illustration. These were included in the synonymy of Alethopteris ambigua by Wagner (1968), but this may have to be revised, at least in part. (Attention is drawn to the strong similarity between Bell’s pl. LXII, fig. 2 and Zodrow & Cleal’s pl. 8, fig. 1.)

Zodrow & Cleal (1998: pl. 2, figs 1-3) figured side by side a pinna of Alethopteris lonchitica (lectotype from Saarland) and a much enlarged specimen showing several fragmentary pinnules from the Sydney Basin in Nova Scotia which shows a vein density that is at least three times higher. (Note the very different enlargements for these two specimens.) The pinnules from the Sydney Basin seem to belong to the Alethopteris lonchitifolia–missouriensis–westphalensis complex (as Zodrow and Cleal do, in fact, assume), and cannot be attributed to Alethopteris lonchitica.

Since Alethopteris lonchitica is here regarded as identical with Alethopteris friedelii (= Alethopteris ambigua sensu Wagner, 1968, non Zodrow & Cleal, 1998), the specimens attributed to Schlotheim’s species in the literature are practically all to be reassigned. No attempt was made by Zodrow & Cleal (1998) to revise the vast amount of literature in which Alethopteris lonchitica has been named. This is understandable because they described material from the upper Westphalian (of the Sydney Basin in Nova Scotia), whereas most of the records of Alethopteris lonchitica (auctorum) correspond to upper Namurian/lower Westphalian specimens. In the Maritime Provinces of Canada this involves material from the Cumberland Basin (near the Bay of Fundy in Nova Scotia) and coeval strata in the area of Saint John (New Brunswick). Specimens from these areas were recorded as Alethopteris lonchitica by Stopes (1914) and Bell (1944, 1966). Both authors admitted Alethopteris discrepans as a synonym. This is a species described from the “Fern Ledges” at Saint John. (N.B. Dawson’s type specimens are very fragmentary.)

Attention is drawn to Alethopteris lancifolia, a species with relatively large pinnules showing a dense nervation
Figure 3. **a**, Enlargement (x 3) of part of the smaller penultimate pinna fragment of holotype (Fig. 2) showing the transition between last order pinna with elongate terminals and almost parallel-sided elongate pinnules in near-terminal position. **b**, A single pinna of holotype with average size lateral pinnules (x 3). N.B. Note compression borders. Repository: Palaeontology Unit, British Geological Survey, Keyworth.
similar to that of \textit{Alethopteris lonchitica sensu} Zeiller (see Buïsine, 1961). This species, originally described from lower Westphalian strata in South Limburg in the Netherlands (Wagner, 1961), has most recently been recorded from the “Fern Ledges”, New Brunswick (Wagner, 2005). It is unclear whether or not this species should be included in the range of variation of \textit{Alethopteris urophylla}. The present writers provisionally exclude this species on the basis of its relatively broader pinnules of generally larger size.

Another species which has been recorded in the literature with specimens comparable to \textit{Alethopteris lonchitica (auctorum)} is \textit{Alethopteris decurrens}. It appears that the range of variation admitted for \textit{Alethopteris decurrens} in the literature may be excessive and that material of \textit{Alethopteris lonchitica (auctorum)} has been included. These more doubtful records will be analysed in the present paper.

It may be that \textit{Alethopteris heterophylla} (Lindley & Hutton, 1832) Göppert, 1836, from Felling Colliery in Northumberland, England, is the same as \textit{Alethopteris urophylla} and \textit{Alethopteris lonchitica (auctorum)}. This assumption is reflected in Kidston (1886: 133) and in the Catalogue of the Hutton Collection published by Hose in 1888, where \textit{Pecopteris heterophylla} appears as a synonym of \textit{Alethopteris lonchitica}. However, Crookall (1955: 26) regarded Lindley & Hutton’s species as a synonym of \textit{Alethopteris decurrens}, a similar species to \textit{Alethopteris urophylla}, with generally more slender pinnules showing a wider, less regular venation. This may be the correct identification, although some doubt remains. It is noted that another one of the synonyms quoted by Hosey is \textit{Alethopteris urophylla}. Lindley and Hutton’s description of \textit{Alethopteris heterophylla} predates Brongniart’s \textit{Alethopteris urophylla}, and if these two species should prove to be identical, it is Lindley and Hutton’s epithet which may be the correct one for the mainly lower Westphalian species recorded generally as \textit{Alethopteris lonchitica (auctorum)}. Unfortunately, the type of \textit{Pecopteris heterophylla} is the specimen illustrated photographically by Zodrow & Cleal (1998) on their pl. 2, figs 1-2. It represents a pinna fragment which apparently terminates in a large apical pinnule. This is how it was depicted by Schlotheim (1804: Taf. XI, fig. 22). However, the photograph is less clear in this respect, and a re-examination of the specimen by M. Barthel, at the present writers’ request, has shown that organic connection cannot be proved. The near-terminal part of the pinna is damaged, and it is noted that the apparent apical pinnule closely resembles a standard lateral pinnule. A fortuitous superposition belongs to the possibilities. Its size and shape does not fit for any of the upper Westphalian species of \textit{Alethopteris} from Saarland. Unfortunately, the lectotype does not lend itself to preparation (M. Barthel, pers. comm.).

Zodrow & Cleal (1998) illustrated photographically the various pinna fragments of Schlotheim’s specimen from Saarland, but they did not provide a description. Instead, specimens from the Sydney Coalfield in Nova Scotia were described on the assumption that these would coincide with Schlotheim’s species. This seems questionable. Their pl. 2, fig. 3 (same specimen as in Bell, 1938: pl. LXI, fig. 5 – as \textit{Alethopteris lonchitica}) shows several pinnule fragments with a higher vein density than the lectotype. Although quite fragmentary, it seems likely that this specimen belongs to the \textit{Alethopteris lonchitifolia–missouriensis–westphalensis complex}. Zodrow & Cleal (1998: 72) indeed assumed that \textit{Alethopteris lonchitifolia} would be the same as \textit{Alethopteris lonchitica}, thus accepting without question the opinion expressed by Thomas & Cleal (1993a: 115). They did not consider any other alternative, such as \textit{Alethopteris friedelii} (= \textit{Alethopteris pseudoaquilina Potonić}, 1893) which they regarded as a probable synonym of \textit{Alethopteris grandinii} (Brongniart, 1828) Göppert, 1836 (see Zodrow & Cleal, 1998: 96).

The assumption that \textit{Alethopteris lonchitica} would be identifiable with \textit{Alethopteris lonchitifolia} has led to a description by Zodrow and Cleal which is only applicable to the \textit{Alethopteris lonchitifolia–missouriensis–westphalensis complex}. This is unfortunate, because it seems likely that the type \textit{Alethopteris lonchitica} belongs to the same species as \textit{Alethopteris ambiguа} (= \textit{Alethopteris pseudoaquilina, Alethopteris friedelii}). The problem is compounded by an emended diagnosis for \textit{Alethopteris ambiguа} as proposed by Zodrow & Cleal (1998: 97) who incorporated,

**COMMENTS ON THE IDENTITY OF**

**Alethopteris lonchitica SCHLOTHEIM EX STERNBERG**

Although the type specimen is in the Museum für Naturkunde, Berlin, Schlotheim’s species was validated by Sternberg (1825). It thus merited inclusion in the Catalogue published by Kvaček & Straková (1997), who noted that the drawing produced by Schlotheim (1804) contained elements from two different sides of the same specimen, an ironstone nodule (“Sphaerosiderit” – \textit{fide} M. Barthel, pers. comm. 20-06-2008). Altogether, fragments of 8 different pinnae of the last order were illustrated, among which Kvaček and Straková selected as the lectotype a fragment on the right hand side of the illustration (which occurs as a single fragment on one face of the rock specimen). This is the specimen illustrated photographically by Zodrow & Cleal (1998) on their pl. 2, figs 1-2. It represents a pinna fragment which apparently terminates in a large apical pinnule. This is how it was depicted by Schlotheim (1804: Taf. XI, fig. 22). However, the photograph is less clear in this respect, and a re-examination of the specimen by M. Barthel, at the present writers’ request, has shown that organic connection cannot be proved. The near-terminal part of the pinna is damaged, and it is noted that the apparent apical pinnule closely resembles a standard lateral pinnule. A fortuitous superposition belongs to the possibilities. Its size and shape does not fit for any of the upper Westphalian species of \textit{Alethopteris} from Saarland. Unfortunately, the lectotype does not lend itself to preparation (M. Barthel, pers. comm.).

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albeit tentatively, *Alethopteris lesquereuxii*, a similar but not identical species. Indeed, Zodrow & Cleal (1998) illustrated specimens of *Alethopteris lesquereuxii* from the Sydney Basin in Nova Scotia as *Alethopteris ambiguа*. This is similar material to that figured by Wagner (1968) as *Alethopteris ambiguа* var. *gibsonii*, also from the Sydney Basin.

It is here concluded that *Alethopteris lonchitica*, as typified by Schlotheim’s type specimen from Saarland, is the same as *Alethopteris ambiguа* (syonyms: *Alethopteris pseudoaquilina*, *Alethopteris friedelii*), a widespread element of upper Westphalian floras. The similar species, *Alethopteris lesquereuxii*, is characterised by generally longer pinnules with a more regular venation. It is agreed with Zodrow & Cleal, that the difference is slight (as is apparent by the inclusion of *Alethopteris ambiguа* var. *gibsonii* as figured by Wagner, 1968, in *Alethopteris lesquereuxii*). The proper identity of *Alethopteris gibsonii*, as figured and described by Lesquereux (1879-80), can only be established by a re-examination of Lesquereux’s material. His diagrammatic drawings do not provide an adequate basis for discrimination.

**SYSTEMATIC DESCRIPTION**

The suprageneric taxonomy used in the present paper follows that of Cleal (1993) in “The Fossil Record 2”. In the list of synonymy the following system of annotations is used (shortened/simplified from Cleal & Shute, 1995):

* The protologue; § First publication of currently accepted combination; ? References to doubtful specimens due to poor illustration or preservation; *pars*: only part of the specimens published belong to the species; *vide*: the authors have seen the specimen(s).

**Figure 4.** Enlargement (x 3) of part of the larger penultimate pinna of holotype, showing average size lateral pinnules. These are narrowly confluent, asymmetrical due to acroscopic constriction, and nearly biconvex, with compression borders. Repository: Palaeontology Unit, British Geological Survey, Keyworth.
Class CYCADOPSIDA Barnard & Long, 1975
Order TRIGONOCARPALES Seward, 1917 emend. Meyen, 1984
Family Trigonocarpaceae Seward, 1917 emend. Meyen, 1984

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

Type species: Alethopteris lonchitica Schlotheim, 1820 ex Sternberg, 1825

This genus of pteridosperm fronds has been discussed recently by Zodrow & Cleal (1998), who gave the following emended diagnosis: “Bipartite fronds, which may attain large dimensions, up to at least 7 metres long. Primary pinna branches usually tripinnate, with no intercalated pinnules or pinnae on the primary rachis branches or secondary rachises. Rachises usually striate. Pinnules strongly asymmetric, fused at the base, decurrent at the basiscopic side, straight or slightly constricted at the acroscopic side. Pinnule lamina generally rather thick, giving a vaulted aspect to the pinnules. Lobing may be rather abrupt or more gradual, but lobing parts of the frond never seem to predominate. Venation characterized by a well-marked and strongly decurrent midvein and numerous, non-anastomosed laterals that meet the pinnule margin at about right-angles or somewhat obliquely. The

Figure 5. Middle part of a pinna of the penultimate order (x 3), showing relatively large lateral pinnules, which are very narrowly confluent. Origin: Barnsley Seam, Yorkshire, England, lower Duckmantian (loc. 2872). Collected by C.J. Cleal, 1974, from opencast site south of Barnsley. Repository: Centro Paleobotánico, Córdoba.
lateral veins fork at irregular intervals, mostly one time, sometimes by a tripartite division, and occasionally each fork divides again (forking twice). Pinnules hypostomatic. Adaxial epidermis shows little marked differentiation of the cells, except over the midvein. Abaxial epidermis has clearly differentiated cells between the costal and intercostal fields. Stomata restricted to the intercostal fields of the abaxial cuticle are anomocytic, or have only a weakly developed, single ring of subsidiary cells. Trichomes are restricted to the abaxial surface and the midveins."

The size of *Aletho pteris* fronds seems to have been very substantial, as follows from the fragment (less than half the frond) of 1.20 m length recorded by Laveine (1986), who calculated a total frond size of c. 7 m.

The genus *Aletho pteris*, as defined above in its restricted sense, does not include *Macraletho pteris* Jongmans & Gothan, 1935, a genus which is virtually restricted to its type species, *Macraletho pteris hallei* Jongmans & Gothan, 1935 (see comments in Wagner, 1968: 21-22). This is an East Asian (Cathaysian) species of Pennsylvanian age, although recorded also in upper Mississippian strata and extending into lowermost Permian. It is fairly closely circumscribed morphologically. It forms a natural unit with *Lonchorhaphidium* (Gothan, 1909 – as a subgroup of *Lonchotis*) Bode, 1941 (as a separate genus), and *Lonchotis* Brongniart, 1828a. The little evidence that is available on reproductive organs, suggests that *Neuralitho pteris* Cremer, 1893 also belongs to the same natural unit (compare Buisine, 1961; Goubet et al., 2000).

The type species, *Aletho pteris lonchitica*, has given rise to taxonomic problems as detailed in the present paper.

**Aletho pteris urophylla** (Brongniart, 1834)
Göppert, 1836
Figs 1-12

? 1836 *Aletho pteris urophylla* (Lindley & Hutton) Göppert, 297.
§ 1836 *Aletho pteris urophylla* (Brongniart) Göppert, 300.
p 1848 *Pecopteris lonchitica*: Sauveur, pl. XL, fig. 3; pl. XXII, fig. 4 (?) (may be either *Aletho pteris urophylla* or *Aletho pteris decurrens*); non pl. XXI, figs 1, 2 (= Neuralitho pteris schlehanki (Stur, 1877) Cremer, 1893); non pl. XXII, fig 5 (= Neuralitho pteris sp. indet.).
* 1848 *Pecopteris multiformis* Sauveur, Pl. XXXVI, fig. 1 (placed in synonymy with *Aletho pteris lonchitica*) by Kidston, 1886: 134.
* 1862 *Pecopteris (Aletho pteris) decurrens* sp. nov. (non Artis); Dawson, 322, pl. XV, figs 40a-c [diagrammatic drawings of very fragmentary specimens; the homonym *Pecopteris (Aletho pteris) decurrens* was changed to *Pecopteris discrepans* by Dawson in 1863; Stopes, 1914, referred *Pecopteris* (*Aletho pteris*) discrepans to *Aletho pteris lonchitica*, meaning *Aletho pteris lonchitica auctorum*).
* 1862 *Pecopteris (Aletho pteris) ingens* sp. nov.; Dawson, 322, pl. XV, figs 41a, b, [drawings of fragmentary pinnules which probably belong to *Aletho pteris lonchitica* (*auctorum*) – see the exhaustive comments by Stopes, 1914: 95-96).
* 1863 *Pecopteris discrepans* Dawson, 468 (name change on the basis of homonymy with *Pecopteris discrepans* Lesquereux – see Lesquereux in Rogers, 1858; however, the real homonym is *Filicites discrepans* = *Aletho pteris discrepans*).
1865 *Aletho pteris discrepans* Dawson; in Hartt in Bailey’s Report, 136-137.
1868 *Aletho pteris discrepans* Dawson; in Hartt, 552-553, fig. 192 1 (copy of the drawing in Dawson, 1862: pl. XV, fig. 40a).
p 1868 *Aletho pteris lonchitidis* Sternberg (as *Aletho pteris lonchitides* in plate explanations); Roehl, Taf. XIV, figs 2, 4, figs 1, 3, 3a (?); non Taf. XXXI, figs 4, 4a (= *Neuralitho pteris* sp. indet.).
1868 *Aletho pteris urophylla* Göppert (sic); Roehl, 75, Taf. XXII, fig. 7.
p 1868 *Aletho pteris heterophylla* Göppert (sic); Roehl, Taf. XXXII, figs 2, 9; non Taf. XXXII, figs 5A, B, 5B(possibly *Neuralitho pteris lonchitifoliata*?); non fig. 203? [cannot be judged properly; nervation as drawn by Dawson resembles that of *Neuropteris obliqua* (Brongniart, 1834) Göppert, 1848].
p 1871 *Aletho pteris discrepans* Dawson; in Hartt, 54, pl. XVIII, fig. 204 (specimen refuged photographically by Stopes, 1914, pl. XIII, fig. 3); non fig. 205? (possibly *Aletho pteris lonchitifoliata*?); non fig. 205? [cannot be judged properly; nervation as drawn by Dawson resembles that of *Neuropteris obliqua* (Brongniart, 1834) Göppert, 1848].
1886-88 *Aletho pteris lonchitica* Schlotho,; Zeiller, 225-228, pl. XXXII, figs 1, 1A (reproduced in Gothan & Franke, 1929, Taf. 12; Zeiller’s figures are partially reproduced in Ralli, 1933: pl. XVI, figs 3, 3a).
1899 *Aletho pteris lonchitica* Brongniart; Hoffman & Ryba, Taf. VIII, figs 1, 1a (same as Brongniart, 1833: pl. 84, figs 1, 1A).
1901 *Aletho pteris lonchitica* Schlothoheim; Kidston, 195, pl. XXII, figs 2, 3.
1907a *Alethopteris lonchitica* Schlotheim; Zalessky, 397-398, Tab. XVI, fig. 6 [Zalessky & Tchirkova, 1938, included this specimen in their synonymy of *Alethopteris davreuxii* (Brongniart, 1828) Göppert, 1836].

1907a *Alethopteris decurrens* Artis; Zalessky, Tab. XVI, fig. 5 (only cited in the plate explanation).

1907b *Alethopteris decurrens* Artis; Zalessky, 467-468, Tab. XVIII, figs 1, 4.

1907b *Alethopteris Serlii* Brongniart; Zalessky, 469-470, Tab. XXI, fig. 2 (included by Zalessky & Tchirkova, 1938, in *Alethopteris lonchitica* – erroneously cited as fig. 1).

p 1910 *Johannophyton discrepans* n. gen. Dawson sp.; Matthew, 83, pl. III, figs 1, 2, 4 (copies of Dawson, 1871: pl. XVIII, figs 203-205), figs 3, 5 (diagrammatic drawings), fig. 6 (diagrammatic drawing), fig. 9; non figs 8, 10 (sporangia); non pl. II, fig. 7 (= *Alethopteris lancifolia* acc. to Wagner, 2005: 16); non figs 8-9 (sporangia).

1910 *Alethopteris lonchitica* Schlotheim; Seward, 553, 574, fig. 290A (after Zeiller, 1886: pl. XXXI, fig. 1A), fig. 364A.

1913a *Alethopteris lonchitica*; Franke in Potonié, 161, Fig. 1, Fig. 2 (after Zeiller, 1886: pl. XXXI, fig. 1), Fig. 3 (drawing).

1913 *Alethopteris lonchitica* Schlotheim; Gothan, 175-177, Taf. 39, fig. 1 (after Franke in Potonié, 1913a: Fig. 1); Taf. 40, fig. 3 (diagrammatic drawing of a pinnule from the specimen figured on Taf. 39, fig. 1).

1913-14 *Alethopteris Serlii* Brongniart; Bureau, 322-323 (excluding synonymy), pl. LXXIX, fig. 6.

p 1914 *Alethopteris lonchitica* Schlotheim (= *Alethopteris discrepans* Dawson); Stopes, 47-53, pl. XII, fig. 30, pl. XIII, fig. 31 (photographic illustration of the specimen figured by Dawson, 1871: pl. XVIII, fig. 240), figs 32, 33 (rather poorly preserved fragments which cannot be judged adequately from the illustration); non pl. XXII, fig. 57A (pinnule fragment with widely confluent pinnules of *Alethopteris* sp. indet.); textfigs 8A-C (rather diagrammatic drawings); non pl. XVIII, fig. 46 (sporangia, and pinnule fragments which may belong to either *Alethopteris* sp. or *Neuralaethopteris* sp.).

1915 *Alethopteris Serli* Brongniart; Gothan & Jongmans in Jongmans, 173, Taf. V, fig. 1.

1916 *Alethopteris lonchitica* Schlotheim; Kidston, pl. XIII, fig. 6.

1923 *Alethopteris lonchitica*; Scott, 172, fig. 69 (although reduced in size and poorly figured, it seems referable to *Alethopteris urophylla*).

1928 *Alethopteris lonchitica*; Jongmans, 15, Plaat 7, fig. 1.

1928 *Alethopteris lonchitica* Schlotheim; Šusta, 439, Taf. XXXIV, Abb. 3. Taf. XXXV, Abb. 3 [as *Alethopteris lonchitica* (valida?) in the plate explanation].

p 1928 *Alethopteris Serli* Brongniart; Šusta, Taf. XXXVI, Abb. 1, 2; non Taf. XXXIV, Abb. 1 (= *Neuralaethopteris*?), Abb. 5 (to *Alethopteris havlenae* Šimůnek, 1996 acc. to Šimůnek, 1996); non Taf. XXXV, Abb. 5 (may also be referred to *Alethopteris havlenae*).

? 1928 *Alethopteris* species; de Voogd, 23, Taf. III, fig. 19.

1929 *Alethopteris lonchitica* (Schlotheim); Crookall, p. 58, pl. XXX., fig. e.

1932 *Alethopteris lonchitica*; Jongmans, 9, 13, Fig. 32.

1932 *Alethopteris lonchitica* Zeiller; Corsin, 18, pl. VIII, figs 1, 1a; texte-fig. 7.

1938 *Alethopteris lonchitica* (Schlotheim); Renier & Stockmans in Renier et al., 85, pl. 75.

1938 *Alethopteris lonchitica* (Schlotheim); Zalessky & Tchirkova, 46-47, 157, fig. 54.

1939a *Alethopteris lonchitica* Schlotheim; Jongmans, Taf. XXIII, figs 57-59; Taf. XXIV, fig. 64; Taf. XXV, fig. 69.

1949 *Alethopteris Helenae* Lesquereux; Arnold, p. 188-189, pl. XIX, figs 5, 6.

p 1949 *Alethopteris decurrens*; Arnold, pl. XIX, fig. 7; non pl. XIX, fig. 4 (pinna terminal).

1951 *Alethopteris lonchitica* (Schlotheim); Stockmans & Willière, pl. C, figs 6, 6a.

? 1951 *Alethopteris lonchitica* (Schlotheim) Göppert; Novik, Tab. LVII, figs 7, 8 (poorly figured and difficult to judge).

p 1952-53 *Alethopteris lonchitica* (Schlotheim); Stockmans & Willière, 239-240, pl. XXVIII, figs 14, 14a (after Stockmans & Willière, 1951: pl. C, figs 6, 6a), pl. L, fig. 7; non pl. L, figs 8-10 (= *Alethopteris cf. decurrens*); non pl. LII, figs 6-9 (too fragmentary to be judged properly).

1952-53 cf. *Aulacotheca Idelbergeri* Halle; Stockmans & Willière, pl. L, fig. 6 (pinnule fragment figured alongside *Aulacotheca synangium*).

p 1953 *Alethopteris lonchitica* (Schlotheim) Unger incl. f. *Serli* (Brongniart); Gothan, 16-18, Taf. 4, fig. 2, fig. 5 (previously published as a drawing by Franke in Potonié, 1913a: Fig. 3, and Gothan & Franke, 1929: Abb. 9); Taf. 5, figs 1, 4, 5; Taf. 6, figs 2-4; non Taf. 4, fig. 1 (= *Alethopteris lancifolia* acc. to Wagner, 1961, 1968, and Wagner, 2005), fig. 3 (= *Alethopteris lancifolia*?); fig. 4 (as f. *Serli*; = *Alethopteris westphalensis* acc. to Wagner, 1968: 154); non Taf. 5, figs 2, 2a (to be compared with *Alethopteris westphalensis*), fig. 3 (= *Alethopteris cf. grandinitoides* Kessler, 1916 = *Alethopteris pseudograndidinitoides* Zodrow & Cleal, 1998); non Taf. 6, fig. 1 (as f. *Serli*; possibly *Alethopteris westphalensis* acc. to Wagner, 1968: 154 – previously figured as a drawing by Franke, 1912 and Franke in Potonié, 1913b as *Alethopteris serli* forma *platyrachis* n.f.).

1953a *Alethopteris lonchitica* Schlotheim; Jongmans, 24, pl. 8, figs 47-49a.

? 1954 *Alethopteris lonchitica* (Schlotheim) Göppert; Novik, Tab. XIX, fig. 5 (difficult to judge from the figuration).

p 1955 *Alethopteris lonchitica* Schlotheim; Crookall, 22-26 (excluding synonymy), pl. V, fig. 2; pl. X, fig. 1 (the complete specimen, partially figured at x ½ size in Seward’s text-book, 1910: fig. 364A), fig. 3; text-
fig. 14H; *non* pl. V, fig. 1 (= *Alethopteris lancifolia* acc. to Wagner, 1961, 1968, and Wagner, 2005); *non* text-fig. 7 (copy of original figure of *Filicites lonchiticus*).

1957 *Alethopteris lonchitica* Schlotheim; Gothan & Remy, 118-119, Abb. 110 (after Franke in Potonié, 1913a, and Gothan, 1953: Taf. 4, fig. 5), Abb. 111.

1957 *Alethopteris lonchitica* Schlotheim; Purkyňová, Tab. III, figs 3, 6.

*?* 1957 *Alethopteris lonchitica* (Schlotheim) Zeiller; Stopa, 83-84, 191, pl. XXXI, fig. 7 (difficult to judge from the photograph).

1958 *Alethopteris lonchitica* (Schlotheim); Stockmans & Willière, pl. IV, figs 2-3.

p 1961 *Alethopteris lonchitica* (Schlotheim) Zeiller; Buisine, 99-115, pl. XIII, fig. 1 (refigured in Figs 8-10 of the present paper); pl. XIII, figs 2-2b; pls XIV-XVI; pl. XVII, fig. 2, 4; pl. XVIII, figs 1-1b; pls XIX, XX; text-figs 9a-c; *non* pl. XVII, figs 1, 3 (= *Alethopteris densinervosa*); *non* pl. XVIII, fig. 2 (= *Alethopteris densinervosa*).

p 1961 *Alethopteris sertl* Brongniart; Buisine, pl. VIII, figs 2, 2a (= *Alethopteris urophylla* acc. to Wagner 1968: 59, 139); *non* pls I-VII, pl. VIII, figs 1, 1a (= *Alethopteris densinervosa* acc. to Wagner, 1968: 59); *non* pl. IX, figs 1, 1a (= *Alethopteris westphalensis* acc. to Wagner, 1968); *non* pl. X, figs 1, 1a, 3-4 (= *Alethopteris densinervosa* acc. to Wagner, 1968); *non* pl. IX, figs 1, 1a, pl. X, figs 2, 2a, pl. XI, figs 1-2, pl. XII, figs 1a-1c (= *Alethopteris westphalensis* acc. to Wagner, 1968).

1961 *Alethopteris lonchitica* (Schlotheim) Unger (sic); Josten, Taf. 10, Fig. 4.

p 1961 *Aulacotheca hallei* Hemingway; Stockmans & Willière, pl. IX, fig. 12 (pinna fragment illustrated alongside *Aulacotheca* synangium).

1962 *Alethopteris lonchitica* Schlotheim; Purkyňová, 75-76, 113, fig. 41b, Tab. XX, fig. 5.

1964 *Alethopteris lonchitica* (Schlotheim) Unger (sic); Drägert, 40, Taf. 2, fig. 3.

p 1965 *Alethopteris lonchitica* (Schlotheim); Stockmans & Willière, Pl. V, figs 3-3a (fragmentary); *non* figs 4, 4a (= *Alethopteris havlena*).

1966 *Alethopteris decurrens* Artis; Migier, 85, 89, Tab. VIII, figs 3-4.

v 1966 *Alethopteris lonchitica* (Schlotheim) Göppert; Bell, pl. VII, fig. 4.

p 1969 *Alethopteris* sp.; Daber, 260, Taf. IX, Bild 7; *non* Taf. I, Bild 1 (cannot be judged from the photograph).

p 1970 *Alethopteris lonchitica* (Schlotheim) *f. typica* Gothan; Havlena, pl. I, figs 10, 11; *non* pl. I, fig. 12 (too fragmentary to be judged properly).

1971 *Alethopteris lonchitica* Schlotheim; Purkyňová, 141, Tab. VII, figs 1-2

p 1972 *Alethopteris lonchitica* Schlotheim; Migier, 145, 157, Tab. XIV, fig. 4; *non* Tab. XIII, fig. 5 (? – cannot be judged properly from the illustration).

1973 *Alethopteris sertl* Brongniart; Biotouianu, pl. II, fig. 13.

1974 *Neuralalethopteris jongmansii* Laveine; Fiebig & Leggewie, Taf. 4, fig. 7.

1975 *Alethopteris decurrens* Artis; van Amerom & Lambrecht, p. 153, 156, Taf. VI, figs 5a, b.

1975 *Alethopteris lonchitica* (Schlotheim) Sternberg; van Amerom, pl. 1, figs 4, 5; pl. 1, figs c, d (diagrammatic drawings).

1977 *Alethopteris lonchitica* (Schlotheim) Zeiller; Purkyňová, 291, 295, pl. IV, fig. 2 (after Purkyňová, 1971: Tab. VII, figs 1, 1a).

1977 *Alethopteris lonchitica* (Schlotheim) Sternberg; Remy & Remy, 272-273, Bild 149a (after Gothan & Remy, 1957: Abb. 111), Bild 149b (after Gothan & Remy, 1957: Abb. 110), Bild 149c (nervation diagram).

1977 *Alethopteris lonchitica* auct. (non Schlotheim?); Scott, 461, pl. 51, fig. 1 (refigured as *Alethopteris* sp. in Scott & Smith, 1977, pl. 2, fig. 3, figs 2, 3, 11, 12).

*?* 1977 *Alethopteris lonchitica* (Schlotheim); Tenčov, 55-56, Taf. XVIII, Bild 5.

v 1981 *Alethopteris urophylla* (Brongniart); Wagner in Mamet & Martínez, 110.

v 1983 *Alethopteris lonchitica* (Von Schlotheim) Zeiller; Wagner, 157.

v 1983 *Alethopteris urophylla* (Brongniart) Von Roehl (sic); Wagner, 157.

v 1983 *Alethopteris cf. michauxii* Buisine; Wagner in Wagner et al., 35 (same as in Wagner & Bowman, 1983).

1984 *Alethopteris lonchitica* (Schlotheim) Zeiller; Havlena, 371-372, pl. I, fig. 1 (same as in Havlena, 1970: pl. I, figs 10, 11); pl. II, fig. 1, figs 4, 5 (? – also to be compared with *Alethopteris davreuwi*); pl. III, figs 1-3, 7-9; pl. IV, figs 1, 4, 5; *non* pl. III, fig. 6 (? – fragmentary; same as in Havlena, 1970: pl. I, fig. 12).

v 1984 *Alethopteris cf. michauxii* Buisine; Wagner in Wagner et al., 35 (same as in Wagner & Bowman, 1983).

1985 *Alethopteris lonchitica* (Schlotheim); Delvolvé & Laveine, 293-294, pl. A, fig. 2, pl. 6, fig. 4.

p 1985 *Alethopteris lonchitica* (Schlotheim) Sternberg; Gillespie & Rheams, 194, 195, pl. II, fig. 2; *non* pl. I, fig. 3 (to be compared with *Alethopteris valida*).

1989 *Alethopteris lonchitica* (Schlotheim) Sternberg; Gillespie et al., 5, pl. 2, fig. 7.

1990 *Alethopteris lonchitica* Schlotheim; Purkyňová, 219-220, Tab. II, fig. 4, Tab. II, fig. 5 (after Purkyňová, 1962: Tab. XX, fig. 5).

1991 *Alethopteris lonchitica* (Schlotheim) Sternberg; Josten, 291-293, Taf. 158, figs 1a, 1b, Taf. 159.

1993a *Alethopteris urophylla* (Brongniart) Presl in Sternberg; Thomas & Cleal, 115, Fig. 4A (same as in Thomas & Cleal, 1993b: 21, left figure); Figs 4B, 5A.

1994 *Alethopteris urophylla*; Cleal & Thomas, 125, pl. 20 (the same specimen as figured in Thomas & Cleal, 1993a and 1993b), text-fig. 61A (after Crookall, 1955).
v 1995 *Alethopteris lonchitica* Brongniart non von Schlotheim; Álvarez-Vázquez, 57-59, lám. 14, figs 1-3; lám. 15, figs 1a, 1b.

1995 *Alethopteris lonchitica* Schlotheim; Brousmiche-Delcambre, Mercier & Coquel, 336, 338, 339, photo 5, 6.

1995 *Alethopteris lonchitica* (Schlotheim) Zeiller; Kotasewa *d* Dubová-Jachowicz *et al.*., pl. IV, fig. 2.

1995 *Alethopteris lonchitica* (Schlotheim) Sternberg (with cf. in the text); Schultka, 24, Taf. 27, figs 1-3.

1995 *Alethopteris tectensis* Stockmans & Willière; Schultka, 24, Taf. 27, figs 4, 5.

1995 *Alethopteris cf. lancifolia* Wagner; Schultka, 24, Taf. 27, fig. 6.

? 1995 *Alethopteris cf. valida* Boulay; Schultka, 24-25, Taf. 27, figs 7, 8 (fragmentary specimens which are not wholly characteristic of *Alethopteris urophylla*, but certainly not *Alethopteris valida*).

1996 *Alethopteris lonchitica* (Schlotheim). Brousmiche Delcambre, Mercier & Coquel, 83: pl. 3, fig. 7 (same specimen as in Brousmiche-Delcambre *et al.*, 1995: photo 6); pl. 4, figs 1, 1a (same specimen as in Brousmiche-Delcambre *et al.*, 1995: photo 5).

p 1996 *Alethopteris urophylla* (Brongniart) Göppert; Šimůnek, 13-16, pl. X, figs 1, 4 (after Šustá, 1928: Taf. XXXIV, fig. 3), fig. 6 (trichome); pl. XI, fig. 1 (after Purkýňová, 1990: Tab. II, fig. 4), figs 2-7 (cuticles); pl. XII, fig. 1 (? - very fragmentary, difficult to judge), figs 2-4, fig. 5 (?), figs 6-10 (cuticles); pl. XIII, figs 1-8 (cuticles); pl. XIV, fig. 1; text-figs 18-23; non pl. X, figs 2,3 (comparable with *Alethopteris decurrens*; non pl. X, fig. 5 (difficult to judge, but possibly *Alethopteris havlena*); non text-fig. 17 (possibly *Alethopteris havlena*).

1996 *Alethopteris lonchitica* (Schlotheim) Göppert; Fisunenko in Solovieva *et al.*, 63, 68, 97, pl. 29, fig. 8.

1997 *Alethopteris lonchitica* Sternberg; Blake, pl. 2, figs 1-3.

1997 *Alethopteris lonchitica* Schlotheim; Brousmiche Delcambre *et al.*, 173-174, pl. II, figs 7-8 (fragmentary).

1998 *Alethopteris cf. lonchitica* Schlotheim; Brousmiche Delcambre, Mercier & Coquel, 108, pl. 13, figs 11, 12 (very fragmentary).

p 1998 *Alethopteris valida* Boulay; Brousmiche Delcambre, Mercier & Sartori, Pl. III, figs 2, 3 (together with *Neuralethopteris schlehanii*), fig. 4 (with *Pariperis gigantea* (Sternberg, 1823) Gothan, 1953; non p. 554, Pl. III, fig. 1 (= *Alethopteris valida*).

v 2000 *Alethopteris lonchitica*; Álvarez-Vázquez, Figs 2, 4 (name only).

v 2001 *Alethopteris urophylla* Brongniart; Wagner, 63, fig. 60 (same as figured as *Alethopteris lonchitica* by Álvarez-Vázquez, 1995: lám. 14, figs 2, 2a).

? 2002 *Alethopteris urophylla* (Brongniart) Presl; Blake *et al.*, 264, 269, 291, 292, pl. XVIII, figs 3, 5.

2002 *Alethopteris decurrens* (Artis) Zeiller; Blake *et al.*, 264, 268, 291, pl. XVIII, fig. 2.

p 2003 *Alethopteris lonchitica* (Schlotheim) Sternberg; Josten & van Amerom, 49, Taf. 92, figs 1, 4, 5; Taf. 95, fig. 8; non Taf. 92, figs 2, 3 (= *Neuralethopteris* sp. indet.?); non Taf. 93, fig. 1 (included with doubt in *Alethopteris lancifolia* by Wagner, 2005); non Taf. 93, figs 2, 3 (a single specimen to be compared with *Neuralethopteris neuropteroides*).

2003 *Alethopteris lonchitica*; Gil Fernández, 41, Fig. 22.

2004 *Alethopteris lonchitica* Sternberg; Cleal & Thomas, Fig. 5c (fragmentary).

Excludenda

1868 *Alethopteris lonchitidis* Sternberg var. *brevifolia* Roehl, 72, Taf. XXI, fig. 9 (*Alethopteris lonchitidis* var. *brevifolia* in plate explanation) (referred to *Alethopteris valida* by Kidston, 1886: 133, and by Crookall, 1955: 13, with doubts).

1879-80 *Alethopteris lonchitica* Schlotheim; Lesquereux, 177-179, pl. XXVIII, figs 7, 7a (= *Alethopteris lancifolia* – although Lesquereux’s description of veins forking once or simple does not seem to fit).

1904 *Alethopteris lonchitica* (Schlotheim); Arber, 305, pl. 20, figs 11, 15 (= *Neuralethopteris rectineris* (Kidston, 1888) Laveine, 1967 acc. to Laveine, 1967: 120).

1905 *Alethopteris lonchitica* Schlotheim; Vinassa de Regny & Gornati, 483, Tav. XII, figs 10-12 (fragmentary specimens which cannot be judged properly from the photographs published at natural size; but suggestive of *Alethopteris lonchitica = Alethopteris ambigua*; these specimens from the Stephanian of the Carnic Alps were included, with doubt, in the synonymy of *Alethopteris leonensis* by Wagner, 1968, a species which, according to Gillespie & Pfefferkorn, 1986, is synonymous with *Alethopteris virginiana*).

1908 *Alethopteris lonchitica* Schlotheim; Renier, 37, fig. 12(h) (drawing of a single pinnule of a specimen figured more completely by Deltenre in Renier *et al.*, 1910: pl. 92, fig. a) (= *Alethopteris lancifolia*).

1910 *Alethopteris lonchitica* (Schlotheim); Deltenre in Renier *et al.*, pl. 92, fig. a (part of the specimen refigured by Gómez-Alba, 1988: lám. 6, fig. 3) (= *Alethopteris lancifolia*).

1913-14 *Alethopteris lonchitica* Unger (sic); Bureau, 321-322, Pl. LXXIX, fig. 7 (= *Neuralethopteris* sp. indet.), fig. 8 (= *Neuralethopteris*?).

1938 *Alethopteris lonchitica* (Schlotheim); Bell, 67, pl. LXI, fig. 5 (refigured by Zodrow & Cleal, 1998: pl. 2, fig. 3). Fragment showing incomplete pinnules that may be attributed to the *Alethopteris lonchitifolia-westphalensis* complex.

1939 *Alethopteris lonchitica* Schlotheim; Janssen, 143, Fig. 129 (mentioned in Leary, 1976) (difficult to judge from the illustration, but comparable to *Alethopteris lonchitifolia*).

1939b *Alethopteris lonchitica* Schlotheim; Jongmans, 31, 37, Taf. VI, fig. 18 (a fragment showing three pinnules which might belong to *Alethopteris valida*).

1952 *Alethopteris lonchitica* Brongniart (sic); Jongmans, pl. XXI, fig. 149 (fragmentary specimen, poorly figured; either *Neuralethopteris neuropteroides* or *Alethopteris* sp. indet.).

1953b *Alethopteris lonchitica* Schlotheim; Jongmans, 42, 43, pl. 9, figs 41-45a (probably *Neuralethopteris neuro-
Redescription of holotype: A tripinnate fragment of a frond showing near-terminal parts of two pinnae of the penultimate order with elongate pinnules, passing rapidly into pinnae of the last order with strongly vaulted pinnules (i.e. showing a convex limb) which display a compression border. Rachises are straight, only 1-2 mm wide (as corresponds to near-terminal parts of major pinnae). Pinnules attached obliquely, at c. 60-80° angle, very narrowly confluent, slightly asymmetrical, with a sloping base and a marked constriction on the acroscopic side. Last order pinna terminals elongate, parallel-sided but tapering in the upper part, as are the elongate pinnules above the passage to pinnae of the last order. Pinnule length in the terminals diminishes upwards, becoming only slightly longer than the lateral pinnules. Apical pinnules always well individualised. Lateral pinnules parallel-sided to slightly biconvex, with bluntly acuminate apices. Length-breadth ratios 2-3 for standard lateral pinnules, with higher ratios for more elongate pinnules. Pinnule length variable as against more constant width, which varies between

? 2007 Alethopteris lonchitica; Opluštil et al., pl. VIII, fig. 4 [figured at x 0.2, which does not allow the identification to be substantiated. N.B. there are no previous records of Alethopteris lonchitica (auctorum) = Alethopteris urophylla from the Radnice Formation in Central Bohemia. It may be assumed that the authors identified Alethopteris lonchitica with Alethopteris lonchitifolia following Zodrow & Cleal’s, 1998, misidentification; Němejc, 1936, did not record Alethopteris lonchitica from the Radnice measures, but figured specimens of the Alethopteris lonchitifolia-missouriensis-westphalensis complex].

2007 Alethopteris lonchitica Sternberg; Šimůnek, 394, pl. 2, figs 6-8 (cuticles); pl. 5, fig. 2 (= Alethopteris lonchitifolia).

Diagnosis (after Brongniart, 1834): “P. foliis tripinnatifidis; pinnis primarisi apice tantum pinnatifidis, pinnulis linearibus longissimis decurrentibus; inferioris bipinnatifidis pinnis elongatis, in pinnulam linearem maximam desinentibus; pinnulis lateralis sub conformibus, in pinnis inferrioribus majoribus, oblongis, oblongis, oblongus, sub contibus, basi paulum dilatatis, decurrentibus et connatis, integerrimis, linea impressa marginatis; nervio medio angusto apprimato notato, nervulis tenuissimis simplicibus vel plurumque furcatis vix obliquis”.

This translates as follows: Tripinnate frond; terminal of primary pinnae clearly pinnatifid, pinnules long, linear and decurrent: lower bipinnate pinnae elongate, with linear pinnules developed to maximum extent; lateral pinnules subparallel in most of lower pinnae, oblique, oblong, blunt, hardly contiguous, with the base only a little expanded, decurrent and connate, entire, margin distinct; midvein thin but well marked, nervules thin, simple or several times forked, hardly if at all oblique.

Holotype: Tripinnate frond fragment from Merthyr Tydfill, South Wales. British Geological Survey collection Cat. n° 5127A, as figured photographically in the present paper (Figs 2-4).
3 and 4 mm. Midrib straight, well marked, deeply immersed in thick pinnule limb, practically non-decurrent and extending to near the pinnule apex. Lateral veins thin, numerous (difficult to count exactly), fairly regularly disposed, generally once forked, slightly curved near the midrib, relatively straight and reaching the pinnule margin at right angles.

Figure 6. Terminal part of a last order pinnae with elongate, narrowly confluent pinnules, with bluntly acuminate apices. Note the elongate terminal. Origin: Rig Burn, about 2 km southwest of Kirkconnel, Sanquhar Outlier, Southern Uplands, Scotland, lower Duckmantian (loc. 9716). (a) x 1; (b) x 3. Collected by K. Higgs, 1971. Repository: Centro Paleobotánico, Córdoba.
Figure 7. **a**, Pinna of the penultimate order with elongate pinnules and ditto terminal (x 1). **b**, Enlargement (x 3) of part of the same specimen. **c**, Relatively large pinnules (x 3). **d**, Smaller, more average size pinnules (x 3). All specimens from GSC loc. 205 (coll. H.M. Ami, 1899), Springhill Mines, Nova Scotia, Canada, Langsettian. Repository: Geological Survey of Canada, Ottawa.
Figure 8. a. A large frond fragment representing a medial portion transitional to the terminal part of an antepenultimate pinna, at half the natural size (x 0.5). It shows the transition between last order pinnae and pinnules, displaying the apical growth which leads to elongate shapes of apical as well as the lateral pinnules. Specimen figured previously by Buisine, 1961: pl. XIII, fig. 1. Origin: Nord/Pas-de-Calais Coalfield, Aniche, Bernicourt, Cécile Seam, Langsettian. Repository and photograph: Musée de Géologie, Ville de Lille. b. Part of the same specimen (x 3) showing average-sized lateral pinnules with characteristic constriction on the acroscopic side and a narrow limb connecting pinnule bases. The enlargement depicts pinnae in the lower left hand corner of the large specimen of Fig. 8a. Photo: P. De Bleeckere, Musée de Géologie, Ville de Lille.
General description of species (based on the sum total of specimens admitted from the different parts of the world – compare list of synonymy): Large fronds (at least tripinnate) with relatively thin rachises and last order pinnae touching laterally. Pinna terminals elongate, parallel-sided, but tapering in the upper part, and similar to the more elongate pinnules. Lateral pinnules oblique, well separated, decurrent, with narrowly confluent bases (which do not normally constitute a common limb alongside the rachis), parallel-sided but tapering in the upper part, with a bluntly acuminate apex. Pinnule lamina strongly convex (“vaulted”), with thin, but distinct midrib immersed in the lamina. Pinnule length extremely variable, depending on the position in major pinnae, with an abrupt transition between last order pinnae and markedly elongate pinnules in the top part of pinnae of the penultimate order. Pinnule width relatively constant even where pinnule length increases markedly (apical growth). Midrib straight and extending into apical part of pinnules. Lateral veins thin, perpendicular to both midrib and pinnule margin, curving only slightly at the point of departure from the midrib; they are generally once forked, more rarely with a second bifurcation and very rarely simple. Vein density 48-55 veins per cm. Length/breadth ratio extremely variable. Dimensions: 9-45 mm length at 3-5 width.

Comparisons: Aletho pteris decurrens (Artis, 1825) Frech, 1880 has narrower, broadly confluent and, generally, more widely spaced pinnules which tend to be slender and more parallel-sided. The vein density is variable in relation to the pinnule width, but seems to be generally 30-40 veins/cm (N.B. although Buiseine, 1961, mentions a vein density of 40-50 veins/cm, he also characterises the venation as “peu serrée” which is contradictory). The wider spaced veins of Aletho pteris decurrens pinnules seem more irregular than those of Aletho pteris urophylla. However, certain parts of Aletho pteris urophylla, which are characterised by more elongate pinnules, may resemble Aletho pteris decurrens (hence the doubts attached to the drawing of Aletho pteris heterophylla). Kidston (1886: 134) observed gradual transitions between Aletho pteris decurrens and Aletho pteris lonchitica (auctorum), and Crookall (1955) noted their similar stratigraphic range. The species introduced by Stockmans & Willière (1952-53) as Aletho pteris edwardsii (1953: 240; 1952: pl. LVI, figs 9, 9a) and Aletho pteris tectensis (1953: 241; 1952: pl. LVI, figs 8, 8a) from one and the same locality in the Assise d’Andenne, upper Namurian (Yeadonian) of Belgium, and which the present writers regard as probably belonging to one and the same species, are comparable to Aletho pteris decurrens in pinnule shape and size, but apparently possess a wider nervation. Additional specimens of Stockmans & Willière’s species, as figured by Josten (1983) from the middle Namurian of the Ruhr District, western Germany, reinforce this impression.

Aletho pteris lancifolia Wagner is characterised by more tapering, lanceolate pinnules of generally larger size and a basal width which is, on the whole, larger than that of Aletho pteris urophylla. Vein density of 45-50 veins/cm is similar to that of Aletho pteris urophylla. It may be that Aletho pteris lancifolia should be regarded as an extreme form of Aletho pteris urophylla, but this can only be demonstrated in very large frond fragments which are not available at present. The most complete specimens known at present (e.g. that figured here as Figs 8-10) do not show complete morphological overlap. Its stratigraphic occurrence is the same as that for Aletho pteris urophylla. N.B. Two of the specimens figured as co-types of Aletho pteris lancifolia by Wagner (1961: pl. 2, figs 6-7) should be excluded because of pinnule shape, the much wider nervation between pinnules, and a wider venation. A comparison with Aletho pteris valida is suggested. No revision of Aletho pteris lancifolia is attempted here, but compare Wagner (2005).

Aletho pteris corsinii Buiseine (1961: 115-125, pl.s XXI-XXVI) shows pinnules similar in shape and size to those of Aletho pteris urophylla. However, pinnule insertion seems on the whole more perpendicular and the constriction on the acrosopic side is consequently less apparent. Its nervation consists of a well marked midrib and perpendicular lateral veins showing a mixture of simple veins and those forked at the midrib. According to Buiseine (1961: 116), the vein density is c. 30 veins per cm, which is less than that admitted for Aletho pteris urophylla.

Aletho pteris hermetetii Buiseine (1961: 179-184, pl. XLIX) is rather similar to Aletho pteris corsinii. Indeed the pinnules are nearly perpendicular, and therefore lack the more markedly asymmetrical aspect of Aletho pteris urophylla pinnules. Vein density is given as c. 30 veins per cm according to Buiseine, which is the same as that recorded for Aletho pteris corsinii.

Aletho pteris lonchitica Schlotheim ex Sternberg has pinnules of similar size, but, on the whole, a little more slender, parallel-sided, with a more broadly rounded apex, and showing a wide midrib extending to the tip of the pinnule. Its lateral veins are more widely spaced. The pinnules of Aletho pteris lonchitica tend to be more pecopteroid, and more nearly perpendicular to the rachis. Aletho pteris friedelii (= Aletho pteris ambigua) is a synonym of Aletho pteris lonchitica. This is an upper Westphalian species which ranges into basal Stephanian.

The Bolovian species Aletho pteris bertrandii Bouroz, 1956 possesses stiff, almost parallel-sided pinnules, tapering in the upper part, with a pointed apex. The very large, elongate terminals are regarded as characteristic. Its venation is characterised by a distinct, rather wide midrib and

Figure 9. Most of the specimen figured as figure 8a, at natural size (x 1). This shows quite well the transitions between lengthened pinnules in the upper parts of two penultimate pinnae and small pinnae in which the pinnules lengthen by apical growth. Photo: P. De Bleeckere, Musée de Géologie, Ville de Lille.
fairly regularly disposed lateral veins which are generally once forked. Vein density is given by Bouroz (1956: 141) as c. 24-28 veins per cm. The similar species *Alethopteris jankii* Coquel & Laveine (Coquel & Laveine, 1979) possesses even larger pinnules, which are marginally wider and therefore apparently not quite as pointed as in *Alethopteris bertrandii*. However, these differences as observed by Coquel & Laveine (1979) are only minor, and the question may be raised whether these two species should not be regarded as one and the same. Coquel & Laveine (1979) also observed the close resemblance which exists with regard to *Taeniopteris? missouriensis* (White, 1899: 140-144, pl. XL, figs 1-7) which is clearly an *Alethopteris*, and which might well prove to be the same as *Alethopteris bertrandii*. Even the vein density is exactly the same (24-28 veins per cm as mentioned by White, 1899: 141). If White’s species is recognised as an *Alethopteris*, its specific name coincides with that of *Alethopteris serlii* var. *missouriensis* White (which was elevated to species rank by Wagner, 1968), thus producing a nomenclatorial clash. However, since *Alethopteris serlii* var. *missouriensis* is described on page 118 of White’s Memoir, and *Taeniopteris? missouriensis* on page 140 of the same memoir, the former would have priority. It is also noted that White’s illustrations of *Alethopteris* (ex *Taeniopteris?*) *missouriensis* are drawings, which need to be checked on accuracy. In view of the homonymy, it is just as well that *Alethopteris bertrandii* exists.

*Alethopteris densinervosa* Wagner, 1968, an upper Westphalian species from northern France (Bolsovian, lower Asturian), shows more biconvex pinnules which tend to be more bluntly acuminate than those of *Alethopteris urophylla* and which are more widely confluent. It shows generally larger pinnules and thus resembles more closely *Alethopteris lancifolia* (see comments in Wagner, 1968: 62). Vein density is quite similar in all three species.

**Figure 10.** Small fragment of Figs 8a and 9 (x 3). Photo: P. De Bleeckere, Musée de Géologie, Ville de Lille.
Alethopteris westphalensis Wagner, 1968 also shows parallel-sided pinnules which are, on the whole, more broadly confluent than those of Alethopteris urophylla, and which tend to be subperpendicular to the rachis. Its pinnules are less asymmetrical than those of Alethopteris urophylla. Vein density is 30–35 veins per cm (Wagner, 1968: 154). This species is fairly similar in pinnule shape and insertion, as well as the vein density, to Alethopteris corsinii, but shows only occasional simple veins whereas these are recorded as common for Alethopteris corsinii.

Alethopteris brevis Weiss, 1869 (Weiss, 1869-72: 82-83, Taf. XI, fig. 1) is a lower Rotliegend species characterised by narrowly confluent, tapering pinnules with rounded apices and a vaulted limb. Their insertion is subperpendicular to slightly oblique. Although comparable, they are, on the whole, more widely spaced than those of Alethopteris urophylla. The terminals of Alethopteris brevis are characterised by a small apical pinnule, whereas these are elongate in Alethopteris urophylla. Its nervation shows a rather strong midrib (apparently wider than that of Alethopteris urophylla pinnules) and at least once forked, perpendicular lateral veins which are rather widely spaced (c. 30 veins per cm). The above description is based on lower Permian material from Valdeviar in SW Spain (Wagner & Mayoral, 2007). The original description and illustration by Weiss (1869-72) relates to a single specimen from the lower part of the frond and which shows more pecopteroid, perpendicularly inserted pinnules. Pinna fragments of these characteristics also occur in the Valdevar locality, which has yielded about a dozen remains showing the range in morphological variation which is not apparent from Weiss’s illustration.

TAXONOMIC DISCUSSION

There can be no doubt that Alethopteris urophylla, as figured and described by Brongniart (1834), is the same as most specimens recorded as Alethopteris lonchitica in the literature, i.e. Alethopteris lonchitica (auctorum). In fact, Brongniart’s species is almost invariably placed in synonymy with Alethopteris lonchitica as understood by the different authors, i.e. independent from the type of Alethopteris lonchitica which the present writers regard as identical to Alethopteris friedelii (= Alethopteris ambiguа). This species is quite different to Alethopteris lonchitica (auctorum). A question mark is raised with regard to Alethopteris lonchitica as figured by Brongniart (1833). The specimens illustrated by Brongniart (1833: pls 84, 128) are apparently from three different localities, viz. Dudweiler near Sarbrücken, the vicinity of Namur in Belgium, and Newcastle-on-Tyne in northeast England. Brongniart (1833: 275) mentions Schlotheim’s type as coming from Silesia, which is in error because the type specimen of Alethopteris lonchitica originated from Saarland in western Germany. It is possible that at least two of the specimens illustrated by Brongniart, i.e. his pl. 84, figs 2 and 7, which show constricted bases to the pinnules in the lower part of the pinnae, should be assigned to Neuraleteletheris neuropteroides (Šusta, 1927) Josten, 1983. Additional remains (pl. 84, figs 4, 5, 6) might well belong to the same species, thus leaving only Brongniart’s pl. 84, figs 1, 1a as Alethopteris lonchitica (auctorum). It is not immediately obvious how Brongniart distinguished this specimen from Alethopteris urophylla which appears in the comparisons as possessing the same kind of passage from elongate pinnules to pinnae of the last order in the terminal parts of higher order pinnae. Of course, this rapid passage from pinnules to pinnae is not uncommon in Alethopteris in general, although Brongniart’s Alethopteris lonchitica of his plate 84, figs 1, 1a, and the holotype of Alethopteris urophylla do share this character to a marked degree. Brongniart was most interested in comparing with the morphological characters of certain Recent ferns, and referred more particularly to Pteris. After diagnosing “Pecopteris” urophylla (Brongniart, 1834: 290), he mentioned that this species also belonged to the Pteris group, but emphasised what he regarded as distinct traces of marginal fructifications, referring undoubtedly to a compression border as occurs in thick-lined pinnules of Alethopteris. This is clearly apparent in the holotype of Alethopteris urophylla (see Figs 3, 4). Discounting this preservational character, one may well pose the question whether Brongniart’s pl. 84, figs 1, 1a, attributed to Alethopteris lonchitica is not the same species as Alethopteris urophylla. There is no apparent difference in the shape and size of pinnules, and the elongate terminals which are partially visible in Brongniart’s pl. 84, fig. 1, are also identical to those of Alethopteris urophylla. The only possible difference is in the venation which appears a little more widely spaced in Brongniart’s Alethopteris lonchitica (pl. 84, fig. 1a), i.e. c. 30 veins/cm. Alethopteris urophylla has a higher vein density of c. 48-55 veins per cm on the pinnule margin. Brongniart’s drawing shows both once forked and simple veins, which accords rather well with his statement (Brongniart, 1834: 290) of both simple and bifurcate (and even more than once bifurcate) veins in Alethopteris urophylla. Brongniart’s pl. 84, figs 1, 1a (for Alethopteris lonchitica) is here included tentatively in the synonymy of Alethopteris urophylla which seems to have been mainly distinguished on the presence of a compression border, misinterpreted as marginal fructifications. Brongniart’s pl. 128 shows a possibly different species which Wuisine (1961) identified with Alethopteris frieldii. This is the species regarded here as identical with Alethopteris lonchitica.

Alethopteris lonchitica (auctorum) as figured from the lower Westphalian of Europe, seems to have been inspired mainly on the well preserved specimen from the North of France illustrated by Zeiller (1886: pl. XXXI, figs 1, 1a), although usage has been variable. Zeiller’s specimen is
broadly similar to *Alethopteris urophylla*, although there is a suggestion of more biconvex, not quite as parallel-sided pinnules, as occur in the type specimen of *Alethopteris urophylla*. Zeiller’s nervation diagram shows predominantly once to more than once bifurcate nervules with only occasional simple veins. The vein density appears to

Figure 11. **a**, Last order pinna (x 2), with elongate, narrowly confluent pinnules; pinna terminal incomplete. Detached pinnules of *Paripteris gigantea* associated. **b**, Two pinnules of the same specimen, enlarged (x 6) to show the once to twice bifurcate veins. Origin: Cabeza de Vaca opencast site near Belmez, Peñarroya-Belmez-Espiel Coalfield, province Córdoba, Spain, upper Duckmantian (loc. CV-004). Repository: Centro Paleobotánico, Córdoba.
be around 46 veins/cm which accords with that found in *Alethopteris urophylla*. The exhaustive documentation published by Buisine (1961) from the same area of northern France insists on the presence of once and twice bifurcate nerves, with a minimum of 45 veins per cm on the pinnule margin, and an average of about 50 veins/cm. Buisine (1961: 109) seems to admit most of Brongniart’s figures attributed to *Alethopteris lonchitica* as belonging to the species which Zeiller (1886-88) described from northern France, but he excluded the specimen figured in the lower part of Brongniart’s (1833) pl. 128, which he compared with *Alethopteris friedelii*, probably correctly. This, ironically, would be the real *Alethopteris lonchitica*. Although Brongniart’s illustration on pl. 128 leaves room for doubt, one would agree with Buisine that this specimen is not the same as those customarily regarded as *Alethopteris lonchitica (auctorum) (= Alethopteris urophylla)*.

Buisine (1961) also discussed the species *Alethopteris discrepans* Dawson (1862, 1868) as figured more reliably by Stopes (1914), and, in agreement with Stopes, included this species in the synonymy of *Alethopteris lonchitica (auctorum)*. Stopes illustrated material from Dawson’s original locality, the “Fern Ledges” at Saint John, New Brunswick (Canada), as well as even more fragmentary remains from the Joggins section on the Bay of Fundy, Nova Scotia. One of the larger fragments of this species figured originally as a diagrammatic drawing by Dawson (1871) was refigured photographically by Stopes (1914: pl. XIII, fig. 31), who added a further, previously unfigured specimen from the Dawson Collection (op. cit.: pl. XII, fig. 30). Although the venation is unclear, these remains could well belong to *Alethopteris urophylla*. She also figured some additional, very fragmentary remains of *Alethopteris discrepans* from the Joggins section in Nova Scotia (Stopes, 1914: pl. XIII, figs 32, 33). The venation of these specimens is unclear. Better preserved, more complete specimens from the Joggins section were collected more recently by Donald Reid, and made available for description by the present writers. These specimens are similar to *Alethopteris urophylla*, but show relatively broader pinnules which are more broadly confluent and which show a wider nervation. Perhaps, they are to be attributed to *Alethopteris corsinii*. The poorly preserved fragments figured by Stopes might well belong to the same species, but this can only be conjectural. On the other hand, the well preserved specimens figured by Bell (1966) from the Springhill Mines, in the same general area of Nova Scotia, under the name of *Alethopteris lonchitica*, can undoubtedly be assigned to *Alethopteris urophylla* (see also Figs 7a-c in the present paper). A reexamination of various other specimens from the Springhill Mines allows the observation that predominantly once bifurcate veins exist, with an admixture of simple veins, and a vein density of around 25-35 veins/cm. This is markedly lower than that of the material from northern France, and also the type of *Alethopteris urophylla*.

The *Alethopteris serlii* as figured and described by Buisine (1961) from the North of France is not Brongniart’s species as Wagner (1968) has pointed out. Zodrow & Cleal (1998: 79) have recently confirmed that *Alethopteris serlii* has been widely misidentified in the literature. They also mentioned that many authors (e.g. Gotham, 1953) regarded *Alethopteris serlii* as merely a growth form of *Alethopteris lonchitica*, meaning *Alethopteris lonchitica (auctorum)*. Part of Buisine’s *Alethopteris serlii* has been redescribed as *Alethopteris densinervosa* by Wagner (1968). This is a species which Zodrow & Cleal (1998) incorporate with their *Alethopteris lonchitica* (which they identified mistakenly with *Alethopteris lonchitifolia*). *Alethopteris densinervosa* and *Alethopteris lonchitifolia* are closely similar, and have been regarded as possible regional varieties by Wagner (1968). This concept is not discussed by Zodrow & Cleal (1998), who based the intraspecific variation of their species on the analysis made by Scheihing & Pfefferkorn (1980) on the *Alethopteris* remains from a single locality in Pennsylvania. They agree with Scheihing and Pfefferkorn that *Alethopteris densinervosa*, *Alethopteris lonchitifolia*, *Alethopteris missouriensis*, and *Alethopteris westphalensis* are all to be regarded as belonging to a single taxon (*N.B. Scheihing and Pfefferkorn also included *Alethopteris serlii*, which is quite different, as Zodrow and Cleal rightly observed). It is noted here that different species may have partly overlapping characters, a fact that is not taken into account by either Scheihing & Pfefferkorn (1980) or Zodrow & Cleal (1998). Their single (composite?) species was identified with *Alethopteris lonchitica* by Zodrow & Cleal (1998), an identification which is rejected by the present writers. Recognition of a single species as meant by Zodrow and Cleal would imply acceptance of White’s *Alethopteris serlii var. missouriensis* as the taxon enjoying priority in the *Alethopteris missouriensis—A. lonchitifolia—A. westphalensis—A. densinervosa* complex. In this case, all the specimens figured and described by Buisine (1961) as *Alethopteris serlii* would have to be assigned to *Alethopteris missouriensis*. However, this is not the opinion of the present writers, who prefer to distinguish two different taxa in Buisine’s material, viz. *Alethopteris densinervosa* and *Alethopteris westphalensis*. The beautiful set of plates depicting large and well preserved remains of *Alethopteris serlii sensu Buisine (non Brongniart)* from the lower part of the Assise de Bruay (Bolsonian) of northern France, probably represents two different species. One of these is characterised by biconvex to more parallel-sided pinnules (in relation to the length of pinnules) and a rather dense venation. This is the taxon described as *Alethopteris densinervosa* (Wagner, 1968: 59), with a vein density of 40-45 per cm. The other species is characterised by more slender pinnules with a slightly wider nervation and, above all, no apparent constriction on the acrosopic side. This is identified with *Alethopteris westphalensis*. Wagner (1968: 59) singled out a specimen
figured by Buisine (1961) on his pl. VIII, figs 2, 2a, for a tentative assignment to *Aletho pteris urophylla*. This opinion is not maintained by the present writers, who prefer to assign this specimen to *Aletho pteris westphalensis*. The specimen in question shows pinnules which are less constricted on the acroscopic side than is customary for *Aletho pteris urophylla*.

Buisine (1961: 89) compared with *Aletho pteris lonchitica* (actorum) in the sense of Zeiller (1886-88), separating his *Aletho pteris serlii* (i.e. *Aletho pteris densinervosa* and *Aletho pteris westphalensis*) from *Aletho pteris lonchitica* (actorum) (i.e. *Aletho pteris urophylla*), as occurring in northern France, primarily on stratigraphic criteria. However, Buisine also drew attention to the more asymmetrical aspect of the pinnules of *Aletho pteris lonchitica* (sensu Zeiller), showing a marked constriction of the basal part on the acroscopic side. The pinnules of the lower Westphalian species also appeared to be more narrowly confluent than those of the upper Westphalian taxon from northern France (op. cit.).

Crookall (1955) provided an exhaustive account of *Aletho pteris lonchitica* (auctorum), with respect to localities in the British Isles. He included in the synonymy both *Aletho pteris urophylla* and *Aletho pteris discrepans*. Crookall illustrated two specimens from the Barnsley Seam (lower Duckmantian) in Yorkshire (op. cit.: pl. V, fig. 2; pl. X, fig. 1), and a Scottish specimen of apparently the same Duckmantian age (pl. X, fig. 3). All seem to accord well with *Aletho pteris urophylla* as regards pinnule size and shape. The approximate vein density, as measured on the enlargement of Crookall’s pl. X, fig. 3, is around 48 veins/cm. This agrees with the vein density of *Aletho pteris urophylla*. An additional specimen from the Duckmantian of Yorkshire (Crookall, 1955: pl. V, fig. 1) appears to fall outside the range of variation, and has been attributed to *Aletho pteris lancefolia* by Wagner (1961, 1968). Crookall did not express the vein density numerically, but referred to the veins as being numerous. Material from the Barnsley Seam is also figured in the present paper (Fig. 5).

Josten (1991), in his comprehensive account of Westphalian “coal measure” floras of the Ruhr District in western Germany, figured only two specimens of what he called *Aletho pteris lonchitica*. Both are fairly typical of the same Duckmantian age (pl. X, fig. 3). All seem to accord well with *Aletho pteris urophylla*. The approximate vein density, as measured on *Aletho pteris urophylla* (= *Aletho pteris lonchitica* sensu Zeiller, as figured later by Josten, 1991), whereas another (Taf. 4, fig. 1) has been ascribed by Wagner (1961) to his *Aletho pteris lancefolia*. Two additional remains, from the middle Namurian (Taf. 4, fig. 3) and the Bolsovian (Taf. 4, fig. 4), respectively, are tentatively attributed to *Aletho pteris lancifolia* and *Aletho pteris westphalensis*. Gothan (1953: Taf. 5, fig. 3) also figured as *Aletho pteris lonchitica* (forma *serlii*) a specimen which is very different, and comparable to *Aletho pteris grandinioides* Kessler according to Wagner, 1968 (referred to *Aletho pteris pseudograndinioides* by Zodrow & Cleal, 1998). A specimen figured by Franke (1912) as *Aletho pteris serli* forma *platyrrachis* (only a drawing), was illustrated photographically by Gothan (1953: Taf. 6, fig. 1), as *Aletho pteris lonchitica* forma *serli*. This specimen was attributed, with doubt, to *Aletho pteris westphalensis* by Wagner (1968), who commented on this specimen in detail. It may be more properly ascribed to *Aletho pteris havlena*.

*Aletho pteris vulgator* Sternberg, 1825, which is commonly attributed to *Aletho pteris lonchitica* (auctorum), is based on a holotype of unknown origin. This type specimen has been refigured photographically by Kvaček & Štraková (1997: pl. 56, fig. 2) at less than natural size (x 0.75). The slender, parallel-sided pinnules allow a comparison with *Neuraletho pteris neuropteroides*, rather than *Aletho pteris lonchitica* (auctorum). It is here rejected as a possible synonym of *Aletho pteris urophylla*. *Aletho pteris vulgator* was renamed *Aletho pteris sternbergii* by Göppert (1836: 295), an illegitimate name as Kvaček & Štraková (1997) have pointed out. It is noted that Göppert (loc. cit.) compared with the specimens which Brongniart (1833: pl. 84, figs 5-7) figured as *Aletho pteris lonchitica* (pars); these specimens are attributed by the present writers to *Neuraletho pteris neuropteroides*. Ettingshausen (1854) figured as *Aletho pteris sternbergii* a specimen which Wagner (1968) referred to *Aletho pteris missouriensis*. This species is quite different from *Aletho pteris vulgator (= Neuraletho pteris neuropteroides*)?

Although not directly relevant to the synonymy of *Aletho pteris urophylla*, the species “Neuopteris” *distans* Sternberg, 1825, *nomen nudum*, but figured as *Aletho pteris lonchitica* by Kvaček & Kvaček (1992), and Kvaček & Štraková (1997), might belong to either *Aletho pteris lonchitofila* or *Aletho pteris westphalensis*. Sternberg’s type (first figured by Kvaček & Kvaček, 1992) is stated to originate from Eschweiler near Saarbrücken (Kvaček & Štraková, 1997: 65).

**COMMENTS REGARDING THE FIGURED SPECIMENS**

Brongniart’s type specimen from South Wales was figured originally as a lithograph (fide Cleal et al., 2005: 53). A copy of Brongniart’s plate is reproduced here as Fig. 1. It has been taken from the facsimile edition of 1915 (Ed. W. Junk, Berlin). When compared with the photograph of the type specimen in the British Geological Survey Col-
lection (Figs 2-4), it becomes apparent that Brongniart’s artist took certain liberties. The outline of the rock sample was made to look more pretty and, more seriously, the two pinnae were depicted as lying in parallel position, whereas, in fact, they were not exactly. Also, the smaller pinnae were not figured exactly as they were, and this means that certain pinnules were partially restored, as a result of which these pinnules were to some extent idealised. The compression borders visible on the specimen, were lost on the lithograph. Even more strikingly, the partial overlap of last order pinnae in the smaller one of the two penultimate pinnae, is not represented on the lithograph which also shows four side pinnae whereas the specimen also preserved parts of two additional pinnae of the last order, which were omitted by the artist. Although the overall representation is quite reasonable, there is an element of “the artist’s impression”.

The holotype of Alethopteris urophylla shows gradual lengthening of pinnules in the lower part of the larger penultimate pinnule fragment. Pinnules of equivalent size and shape occur in the specimen figured here from Yorkshire, England (Fig. 5), representing the medial part of a pinna of the penultimate order. A lower position in the frond is suggested by the pinna with markedly longer pinnules and ditto terminal depicted by figure 6 (specimen from Sanquhar, Southern Uplands of Scotland). Like the holotype from Merthyr Tydfill, South Wales, it shows slightly asymmetrical pinnules with bluntly acuminate apices and narrowly confluent bases with a marked constriction on the acroscopic side. The dense, fairly regular venation is characteristic. Comparable specimens are depicted by figures 7a-c from the Springhill Mines Formation of the Cumberland Basin in Nova Scotia, Canada. Shorter pinnules of similar characteristics to those of the holotype are shown by figure 7d, also from the Springhill Mines Formation.

Figures 8-10 represent a specimen from the North of France, figured previously by Buisine (1961: pl. XIII, fig. 1). It shows all the transitions from lengthened pinnules to small pinnae, and is more complete than the classical specimen figured by Zeiller (1886: pl. XXXI, fig. 1) from the same locality (veine Cécile).

A specimen from the Peñarroya-Belmez-Espiel Coalfield of SW Spain (Fig. 11a) also shows the longer kind of pinnules tapering into bluntly acuminate apices. The apical pinnule of this pinna fragment is broken off so that its elongate shape is not visible, but must be assumed. The well preserved veining pattern is displayed by figure 11b (at x 6). This allows observing generally once bifurcate lateral veins which are sometimes tripartite or in fours. Simple veins are notably absent. Another fragment, this time from NW Spain (Fig. 12), shows pinnules of similar size and shape, with a fairly regular venation. It is noted that the presence of simple veins is suggested by incomplete preservation near the midrib, where the first vein bifurcation commonly takes place.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

This chapter can only be written as a result of the analysis of the literature as reflected in the list of synonymy for Alethopteris urophylla, and the corresponding records of stratigraphic ranges in the different areas (Fig. 13). With regard to the geographic distribution, it is noted that this refers to North America and Europe, i.e. only part of the Amerosinian Realm (palaeoequatorial belt) of Pennsylvania times. This restriction probably reflects the paucity of records corresponding to the lower Pennsylvanian in Central Asia and China with the adjacent parts of SE Asia. Although conjectural, there is no reason why the widespread Alethopteris urophylla should not occur all over the palaeoequatorial belt.

Within the area where this species has been recorded (generally under the name of Alethopteris lonchitica, auctorum, non von Schlotheim), the westernmost occurrence is in the Michigan Basin of the American Midcontinent. This is situated on the large cratonic area which extends from North America across part of northern Europe to the Russian Platform (including Scandinavia). The most extensive records correspond to the sedimentary basins which were established on and near the margin of this vast cratonic area. This was subjected, in the main, to shallow marine conditions (with cyclothemic deposits – compare Heckel, 1989, 1995, 2003). Basins accumulating predominately non-marine, coal-bearing deposits occur mainly from the Appalachians through the Maritime Provinces of Canada into the British Isles, northern Europe (North of France, Belgium, the Netherlands, West Germany, NE Germany), Poland/Moravia, and, on the southern margin of the Russian Platform, the vast area of the Donbas (Russia/Ukraine). Although there is general agreement on the continuity between North America and Europe (the Atlantic Ocean opened up much later than the Pennsylvanian), the exact fit between the different elements of these two major areas is still subject to discussion. The various palaeotectonic elements involved are still only partly understood and the various reconstructions proposed in the literature are all debatable in detail. This is why the present authors decided against including a map showing localities.

To the South of the basinal areas linked to the cratonic margin referred to, lies the tectonically mobile region of the Hercynian (Variscan) Chain, an area of uplift with continental basins (rift? and strike-slip), which verged onto the cratonic margin. The exact extent southwards of the Hercynian Chain is also subject to discussion, but it is clear that northern Spain (Cantabrian Mountains, Pyrenees), an area on the western edge of the Palaeoetethys, had a different geological history, which is not clearly linked to the Hercynian Chain. On the other hand, the various terranes constituting the Iberian Massif, did originate from areas which may have been linked to NW Eur-
A single occurrence in the Vendée, SW France might be explained in a similar manner. More isolated occurrences, which are not clearly attributable to major palaeotectonic units, lie in the French Alps, Romania and Bulgaria.

Whatever the palaeotectonic conditions may have been, it seems that the composition of Pennsylvanian floras is sufficiently similar throughout the North American and European area, to suggest the absence of oceanic barriers and, by inference, a continuity of land area at times of marine lowstand. *Alethopteris urophylla* is one of the more widespread lower Pennsylvanian floral elements.

A list of geographic locations, as justified by the list of synonymy and Figs 1-12 of the present paper, includes Michigan, Alabama, Georgia, West Virginia (Appalachians), New Brunswick, Nova Scotia (Cumberland Basin), Scotland (Midland Valley and Southern Uplands), England North of the Wales/Brabant Massif, South Wales, NW England North of the Wales/Brabant Massif, South Wales, NW

Figure 12. Near-terminal pinna fragment with elongate pinnules (x 3). Origin: Curavacas Formation at Los Cintos, south slope of Monte Hormigales, province Palencia, NW Spain, lower Duckmantian (loc. 8646). Repository: Centro Paleobotánico, Córdoba.
France, Belgium, Netherlands Limburg, western Germany (Ruhr Coalfield), the NE Germany subsurface, La Vendée in SW France, the French Alps, NW Spain (Cantabrian Mountains), Pyrenees, SW Spain (Sierra Morena), the Upper Silesian Basin of Poland and Moravia (Czech Republic), Rumania, Bulgaria (Svoge Basin), and the Donbass of Ukraine and Russia.

The full stratigraphic ranges cannot always be given for each individual area, since in some cases only isolated records exist. The different nature of the existing records is reflected in the chart of figure 13.

The westernmost occurrence is in the Michigan Basin, situated in the northern Midcontinent of the United States. Arnold (1949) figured and described the Pennsylvanian flora of the Michigan Basin, which covers a range from upper Langsettian to upper Duckmantian, according to his records, and using present-day stratigraphic terminology. He recorded *Alethopteris urophylla* as *Alethopteris helenae* Lesquereux, 1879. This is undoubted the wrong identification. The locality was identified as the Big Charles, probably the “Intermediate Flora” of Arnold (1949: Table I). This might be early Duckmantian.

One of the specimens figured as *Alethopteris lonchitica* from Alabama by Gillespie & Rheams (1985: pl. II, fig. 2) may be attributed to *Alethopteris urophylla*. No exact locality is given, but the total range represented in the Warrior Basin of Alabama is stated to correspond to the New River Formation of the Appalachians (Blake et al., 2002: Fig. 5), of Langsettian age (*op. cit.*). A single fragment figured from Georgia by Gillespie et al. (1989) as *Alethopteris lonchitica* may also be attributed to *Alethopteris urophylla*. The coal-bearing strata in Georgia are regarded as equivalent to part of the New River, i.e. Langsettian (*op. cit.*).

The more complete records from West Virginia (Blake et al., 2002: Fig. 2) show *Alethopteris urophylla* to range from the higher part of the New River Formation to the upper Kanawha, which is regarded as equivalent to upper Langsettian, through Duckmantian into lower Bolsovian.

*Alethopteris urophylla* has been recorded from New Brunswick, Canada, as *Alethopteris discrepans* and *Alethopteris lonchitica*. The locality is “Fern Ledges” at Saint John, which is of Langsettian age (Wagner, 2005). Undoubted records from Nova Scotia, Canada, all refer to the Springhill Mines which worked coal seams of late Langsettian age (according to floral data in the authors’ possession).

The northeastern continuation of Nova Scotia and Newfoundland lies in Scotland where *Alethopteris urophylla* has been documented (as *Alethopteris lonchitica*) from the Central Coalfield in the Midland Valley (Kidston, 1916) and from Sanquhar in the Southern Uplands (see Fig. 6 of the present paper). Kidston’s record refers to Lanarkian, a term which corresponds with upper Yeadonian and lower Langsettian, according to Crookall (1955: Table A). The specimens from Sanquhar are from lower Duckmantian deposits (K. Higgs, pers. comm., 13-11-2007).

More extensive records exist from England and South Wales, both as *Alethopteris lonchitica* (*auctorum*) and *Alethopteris urophylla*. The stratigraphic range of *Alethopteris urophylla* from England North of the Wales-Brabant Massif is from Langsettian to lower Bolsovian according to Cleal (2005). Lower levels, corresponding to the Namurian substages, Marsdenian and Yeadonian, have yielded

![Figure 13. Chart depicting stratigraphic ranges established for the different areas in the palaeoquatorial belt where records of *Alethopteris urophylla* exist.](image-url)
Aletho pteris lonchitica (auctorum), as recorded by Lacey (1952). In the absence of figured specimens, it is difficult to judge these records.

South of the Wales-Brabant Massif there are detailed records from the South Wales Coalfield (Cleal, 2007), showing Aletho pteris urophylla to range from basal Langsettian to about mid-Bolsovian. Arber (1914) and Crookall (1955) mention Aletho pteris lonchitica (auctorum) from the Kent Coalfield in England, which is the lateral continuation of the Nord/Pas-de-Calais Coalfield in northwestern France. The records of Aletho pteris urophylla from Nord/Pas-de-Calais are mainly under the name of Aletho pteris lonchitica (Buisine, 1961), but it seems that some remains identified as Aletho pteris serlii also belong to Aletho pteris urophylla (compare list of synonymy). The ranges given by Buisine (op. cit.) show Aletho pteris lonchitica (auctorum) as mainly occurring in Langsettian and lowermost Duckmantian, with a total range from Yeadonian to upper Duckmantian. The specimen figured by Buisine (1961: pl. VIII, figs 2, 2a) as Aletho pteris serlii, but attributed by the present authors to Aletho pteris urophylla, originated from the Faisceau d’Ernestine, Assise de Bruay, lower Bolsovian.

In Belgium, which continues the area of coal-measures in northwestern France, Aletho pteris lonchitica (auctorum) has been recorded from Marsdenian (lower part of Assise d’Andenne) to Langsettian.

North of the Liège Coalfield area in Belgium lies the South Limburg Coalfield of the Netherlands and the contiguous Aachen Coalfield of western Germany. Fossil records are mainly from South Limburg and boreholes from the deeper subsurface to the North. The lowest occurrence is in the Kinderscoutian near Aachen (de Voogd, 1928). The records from South Limburg include material from Langsettian and lower Duckmantian strata (Gothan & Jongmans in Jongmans, 1915; Jongmans, 1928).

In the Ruhr District and Westphalia (western Germany) there are records of Aletho pteris lonchitica (auctorum) ranging from upper Marsdenian to lower Asturian. The lower part of the range refers to the Namurian B of Hagen-Vorhalle in Westphalia (Schultka, 1995; Josten & van Ame- rom, 2003). All illustrations of this species by Josten refer to material from Langsettian and Duckmantian strata of the Ruhr District. The higher part of the range as given by Josten (2005) refers to the lower Asturian (ex Westphalian D) of the Osnabrück region, as quoted in Josten (1966: 614) from Piesberg. The relevant specimens were not illustrated and since it may be assumed that Josten accepted the large amount of morphological variation admitted by Gothan (1953), it seems likely that forms comparable to Aletho pteris westphalensis are involved. This is why the present writers do not accept a range beyond lower Bolsovian for western Germany.

Very deep boreholes in NE Germany reached coal-bearing strata of Langsettian and Duckmantian ages (Da- ber, 1992). No exact stratigraphic identification is given for the specimen figured as Aletho pteris sp. by Daber (1969), which the present authors include with Aletho- pteris urophylla.

Aletho pteris lonchitica (auctorum) has been recorded repeatedly from the Upper Silesian Basin which extends from southern Poland into the Czech Republic (Moravia). In a range chart from Poland (Kotasowa & Migier, 1995) it is stated that Aletho pteris lonchitica (auctorum) occurs from upper Yeadonian to basal Bolsovian. Purkyňová (1996) indicates that the range of Aletho pteris lonchitica (auctorum) in the Ostrava-Karviná Coalfield (Czech part of the Upper Silesian Basin) extends from high Namurian B (Marsdenian) to Westphalian A (Langsettian).

Two coalfield areas in the Balkans (Rumania, Bulgaria) contain records of Aletho pteris urophylla. The Rumanian material came from Baia Nouă (Siriinia Basin), which was regarded as Westphalian D by Biţoianu (1972a, 1973). However, the presence of several species of Neuraletho- pteris which are misidentified by Biţoianu (e.g. Neuro- pteris ovata Hoffmann, 1826 – Biţoianu, 1973: pl. II, fig. 16, which is most likely referable to Neuraletho pteris jongmansii Laveine, 1967), show that the Langsettian is involved. In Bulgaria, the Svo ge Basin, North of Sofia (Tenčov, 1977), Aletho pteris lonchitica (auctorum) was recorded from the Svidanya Formation of Yeadonian or Langsettian age.

Even further East, on the southern edge of the Russian Platform, lies the large basin of the Donbass. The range of Aletho pteris lonchitica (auctorum) is given by Fissunenko in Solovieva et al. (1996) as embracing most of the Bashkiran (from E limestone) and reaching into middle Moscovian (m1 coal bed). The correlation with West European stratigraphic units is controversial, but it is apparent that this species does not occur in upper Moscovian which would correspond approximately to Bolsovian-Asturian.

Several records of Aletho pteris lonchitica (auctorum) have been published from the French Alps (Briançonnais). These refer to strata assigned to Marsdenian to lower Langsettian (Brousmiche-Delcambre et al., 1995-98).

In SW Europe there are first of all the old records from the Vendée (Bureau, 1913-14). This refers to the lower Westphalian coalfield of Chantonnay, a narrow NW-SE oriented, elongate basin alongside a major (strike-slip?) fault (see map in Mathieu, 1932).

Similar conditions obtain for two lower Westphalian coalfields in the SW Spain, viz. Villanueva del Río y Minas (Sevilla province) and Peña rroaya-Belmex-Espiel (Córdoba province). Both strike NW-SE and the Peña rroaya Basin is clearly controlled by a very major strike-slip fault (intracontinental, transcurrent fault? – see Wagner, 1999). The Villanueva Coalfield contains a small succession (less than a hundred metres) with floral contents indicating a late Langsettian age (see the records in García-Loygorri
& Ortúñ Aznar, 1969, and Ortúñ, 1970, who suggested early Duckmantian). The abundant floral records from the Peñarroya-Belmez-Espiel Coalfield (Álvarez-Vázquez, 1995, 2000) show Alethopteris urophylla to occur in upper Langsettian to upper Duckmantian (and lower Bolsovian?) strata.

In the Cantabrian Mountains of NW Spain the lower Westphalian floras are rarely represented due to the predominant marine facies. The sparse records are from uppermost Langsettian and lower Duckmantian of the Curavacas Conglomerate Formation in northern Palencia (Stockmans & Willière, 1965, and Fig. 12 of the present paper).

The Pyrenees provide only rare floral records of the Namurian-Westphalian interval, due to the predominant marine facies and large gaps in the stratigraphic succession. An important record is that published by Delvolvé & Laveine (1985) from the axial zone (Laruns-Somport map sheet of the French Geological Survey). Goniatite finds from the same horizon have allowed dating their records of Alethopteris lonchitica (auctorum) as Kinderscoutian (R1).

It follows that Alethopteris urophylla ranges from middle Namurian (Kinderscoutian) to lower Bolsovian, with most records referring to Langsettian and Duckmantian strata. This seems to reflect the predominant occurrence of coal-bearing strata in the lower Westphalian, and may not be a true reflection of the principal occurrence of this species.

SUMMARY AND CONCLUSIONS

The common lower Pennsylvanian species Alethopteris urophylla has been shown to be widespread in the coal-bearing facies of the palaeoequatorial belt (Amerosinian Realm). Examples are figured from the British Isles (South Wales, Yorkshire, southern Scotland), Nova Scotia, North of France, NW and SW Spain. The photographic illustration of the holotype shows that Brongniart’s illustrator took certain liberties with the drawing as published in 1834.

Alethopteris urophylla was usually recorded as Alethopteris lonchitica, a species which Zodrow & Cleal (1998) refigured on the basis of its lectotype from the upper Westphalian of Saarland. Unfortunately, their description is based on material from Nova Scotia, which may have been misidentified. Indeed, they identified Alethopteris lonchitica with the Alethopteris lonchitifolia–missouriensis–westphalensis complex, but this seems to have been a mistake. The present writers suggest that the type Alethopteris lonchitica identifies with Alethopteris friedelii, which has also been described from Saar-Lorraine. This species has been placed in synonymy with Alethopteris ambigua by Wagner (1968). The taxonomic revision by Zodrow & Cleal thus needs to be modified. Alethopteris lonchitica is here regarded as synonymous with Alethopteris ambigua (= Alethopteris friedelii), and different to the Alethopteris lonchitifolia–missouriensis–westphalensis complex. Alethopteris lesquereuxii needs to be reinstated and not placed in synonymy with Alethopteris ambigua (= Alethopteris lonchitica), as Zodrow & Cleal suggest, albeit tentatively.

The geographic distribution of this species is shown to range from Michigan in the West to the Donbass in the East.

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