A REVISION OF THE LOWER PENNSYLVANIAN
Alethopteris lonchitica (auctorum) 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 (auctorum) 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 friedelii 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. 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 (auctorum) se identifican, en realidad, con Alethopteris urophylla (Brongniart, 1834) Göppert, 1836. En este trabajo se redescribe 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 Bertrand, 1932; en este trabajo se defiende la sinonimia con Alethopteris friedelii 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

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 shows 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 (Amerosinian 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* (*aurantioidum* (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 Brongniart’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. Gothan (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 subelegans* (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/low 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 *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 *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 *Alethopteris lonchitica* (auctorum) is *Alethopteris decurrens*. It appears that the range of variation admitted for *Alethopteris decurrens* in the literature may be excessive and that material of *Alethopteris lonchitica* (auctorum) has been included. These more doubtful records will be analysed in the present paper.

It may be that *Alethopteris heterophylla* (Lindley & Hutton, 1832) Göppert, 1836, from Fellong Colliery in Northumberland, England, is the same as *Aletho pteris urophylla* and *Aletho pteris lonchitica* (auctorum). This assumption is reflected in Kidston (1886: 133) and in the Catalogue of the Hutton Collection published by Hoswe in 1888, where *Pecopteris heterophylla* appears as a synonym of *Aletho pteris lonchitica*. However, Crookall (1955: 26) regarded Lindley & Hutton’s species as a synonym of *Alethopteris decurrens*, a similar species to *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 Howse is *Aletho pteris urophylla*. Lindley and Hutton’s description of *Alethopteris heterophylla* predates Brongniart’s *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 Howse is *Alethopteris urophylla*. Lindley and Hutton’s description of *Alethopteris heterophylla* predates Brongniart’s *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 *Alethopteris lonchitica* (auctorum). Unfortunately, the type of *Pecopteris heterophylla* is reputedly lost (McLean – *fide* C.J. Cleal, pers. comm. 17-10-2006), and this leaves *Alethopteris urophylla* as the more reasonable choice for typifying the morphospecies recorded in the literature as *Alethopteris lonchitica* (auctorum). Lindley and Hutton’s illustrations are diagrammatic drawings which leave ample room for speculation. It is also noted that the slender pinnules depicted suggest *Alethopteris decurrens* rather than *Alethopteris urophylla*.

**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” – *fide* M. Barthel, pers. comm. 20-06-2008). Altogether, fragments of 8 different pinnules 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 conection 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 *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 *Alethopteris lonchitifolia*) shows several pinnule fragments with a higher vein density than the lectotype. Although quite fragmentary, it seems likely that this specimen belongs to the *Alethopteris lonchitifolia–missouriensis–westphalensis* complex. Zodrow & Cleal (1998: 72) indeed assumed that *Alethopteris lonchitifolia* would be the same as *Alethopteris lonchitica*, thus accepting without question the opinion expressed by Thomas & Cleal (1993a: 115). They did not consider any other alternative, such as *Alethopteris friedelii* (= *Alethopteris pseudoaquilina* Potonié, 1893) which they regarded as a probable synonym of *Alethopteris grandinii* (Brongniart, 1828) Göppert, 1836 (see Zodrow & Cleal, 1998: 96).

The assumption that *Alethopteris lonchitica* would be identifiable with *Alethopteris lonchitifolia* has led to a description by Zodrow and Cleal which is only applicable to the *Alethopteris lonchitifolia–missouriensis–westphalensis* complex. This is unfortunate, because it seems likely that the type *Alethopteris lonchitica* belongs to the same species as *Alethopteris ambiguia* (= *Alethopteris pseudoaquilina*, *Alethopteris friedelii*). The problem is compounded by an emended diagnosis for *Alethopteris ambiguia* as proposed by Zodrow & Cleal (1998: 97) who incorporated,
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* (synonyms: *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; p pars: only part of the specimens published belong to the species; v 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


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 *Alethopteris* 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 7 m.

The genus *Alethopteris*, as defined above in its restricted sense, does not include *Macralethopteris* Jongmans & Gothan, 1935, a genus which is virtually restricted to its type species, *Macralethopteris hallei* Jongmans & Gothan, 1935 (see comments in Wagner, 1968: 21-22). This is an East Asian (Cathaysian) species of Pennsylvanian age. It is noted that several species which have been attributed to *Alethopteris* in the Permian floras of East Asia, China in particular, are subject to reservation. In some cases the genus *Callipteridium* Weiss, 1870, is involved; in other cases the affinities are unclear. *Alethopteris* seems to be essentially Pennsylvanian in 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 *Lonchopteridium* (Gothan, 1909 – as a subgroup of *Lonchopteris*) Bode, 1941 (as a separate genus), and *Lonchopteris* Brongniart, 1828a. The little evidence that is available on reproductive organs, suggests that *Neurallethopteris* Cremer, 1893 also belongs to the same natural unit (compare Buisine, 1961; Goubet et al., 2000).

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

*Alethopteris urophylla* (Brongniart, 1834)

Göppert, 1836

Figs 1-12

- ? 1832 *Pecopteris heterophylla* Lindley & Hutton, 113-114, pl. 38, figs 1-2 (type specimen unavailable and presumably lost).

<table>
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<tr>
<th>Year</th>
<th>Reference</th>
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<td>1836</td>
<td><em>Alethopteris heterophylla</em> (Lindley &amp; Hutton) Göppert, 297.</td>
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<tr>
<td>1836</td>
<td><em>Alethopteris urophylla</em> (Brongniart) Göppert, 300.</td>
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<td>1848</td>
<td><em>Pecopteris lonchitica</em>; Sauveur, pl. XL, fig. 3; pl. XLII, fig. 4 (=? may be either <em>Alethopteris urophylla</em> or <em>Alethopteris discrepans</em>; non pl. XLII, figs 1, 2 (= <em>Neurallethopteris schlehanii</em> (Stur, 1877) Cremer, 1893); non pl. XLII, fig 5 (= <em>Neurallethopteris</em> sp. indet.).</td>
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<tr>
<td>1848</td>
<td><em>Pecopteris multiformis</em> Sauveur, Pl. XXXVI, fig. 1 (placed in synonymy with <em>Alethopteris lonchitica</em> by Kidston, 1886: 134.</td>
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* 1862 *Pecopteris (Alethopteris) discrepans* sp. nov. (non Arts); Dawson, 322, pl. XV, figs 4a-c [diagrammatic drawings of very fragmentary specimens; the homonym *Pecopteris (Alethopteris) discrepans* was changed to *Pecopteris discrepans* by Dawson in 1863; Stopes, 1914, referred *Pecopteris (Alethopteris) discrepans* to *Alethopteris lonchitica*, meaning *Alethopteris lonchitica* auctorum].

* 1862 *Pecopteris (Alethopteris) ingens* sp. nov.; Dawson, 322, pl. XV, figs 41a, b [drawings of fragmentary pinnules which probably belong to *Alethopteris 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* = *Alethopteris discrepans*).

1865 *Alethopteris discrepans* Dawson; in Hartt in Bailey’s Report, 136-137.

1868 *Alethopterys discrepans* Dawson; Dawson, 552-553, fig. 192 i (copy of the drawing in Dawson, 1862: pl. XV, fig. 4a).

* 1868 *Alethopteris lonchitidis* Sternberg (as *Alethopteris lonchitides* in plate explanations); Roehl, Taf. XIV, figs 2, 4, figs 1, 3, 3a (?); non Taf. XXXII, figs 4, 4a (= *Neurallethopteris* sp. indet.).

1868 *Alethopteris urophylla* Göppert (sic); Roehl, 75, Taf. XXII, fig. 7.

* 1868 *Alethopteris heterophylla* Göppert (sic); Roehl, Taf. XXXII, figs 2, 9; non Taf. XXXII, figs 5A, B, 5Ba (could be *Neurallethopteris schlehanii* (Kidston, 1886: 133, placed all these figures in *Alethopteris lonchitica*). *Alethopteris discrepans* Dawson; Dawson, 54, pl. XVIII, fig. 204 (specimen refigured photographically by Stopes, 1914, pl. XIII, fig. 3); non fig. 203? (possibly *Alethopteris lonchitifolia*?); non fig. 205? [cannot be judged properly; nervation as drawn by Dawson resembles that of *Neuropteris obliqua* (Brongniart, 1834) Göppert, 1848].

1886-88 *Alethopteris lonchitica* Schlotheim; Zeiller, 225-228, pl. XXXI, 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 *Alethopteris lonchitica* Brongniart; Hoffman & Ryba, Taf. VIII, figs 1, 1a (same as Brongniart, 1833: pl. 84, figs 1, 1A).
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, fig. 290A (after Zeiller, 1886: pl. XXXI, fig. 1A), fig. 364A.

1913b *Alethopteris lonchitica*; Franko 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 Franko in Potonié, 1913a: Fig. 1); Taf. 40, fig. 3 (diagrammatic drawing of a pinnule from the specimen figured on Taf. 39, fig. 1).

1913-1914 *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 (pinna 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 *Neuralalethopteris* 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 (= *Neuralalethopteris*?), Abb. 5 (to *Alethopteris havlenaе* Šimůnek, 1996 acc. to Šimůnek, 1996); non Taf. XXXV, Abb. 5 (may also be referred to *Alethopteris havlenaе*).

? 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; text-fg. 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. LI, figs 6-9 (too fragmentary to be judged properly).

1952-53 cf. *Aulacotheca Idelbergeri* Halle; Stockmans & Willière, pl. L, fig. 6 (pinna 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. grandinitoidei* Kessler, 1916 = *Alethopteris pseudograndininitoidei* 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 lanceifolia acc. to Wagner, 1961, 1968, and Wagner, 2005); non text-fig. 7 (copy of original figure of Filicites lonchitius).

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

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

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

1958 Alethopteris lonchitius (Schlotheim); Stockmans & Willièire, pl. IV, figs 2-3.

p 1961 Alethopteris lonchitius (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 serlii 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 lonchitius (Schlotheim) Unger (sic); Josten, Taf. 10, Fig. 4.

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

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

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

p 1965 Alethopteris lonchitius (Schlotheim); Stockmans & Willièire, Pl. V, figs 3-3a (fragmentary); non figs 4, 4a (= Alethopteris havelnae).

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

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

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

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

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

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

1973 Alethopteris serlii Brongniart; Biţoianu, pl. II, fig. 13.

1974 Neuralethopteris 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 lonchitius (Schlotheim) Sternberg; van Amerom, pl. 1, figs 4, 5; pl. 1, figs c, d (diagrammatic drawings).

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


p 1977 Alethopteris lonchitius 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 lonchitius (Schlotheim); Tenčov, 55-56, Taf. XVIII, Bild 5.

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


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

v 1983 Alethopteris cf. michauxii Buisine; Wagner in Wagner & Bowman, 154.

1983 Alethopteris lonchitius (Schlotheim) Sternberg; Josten, 128-129, Taf. 47, figs 1, 1a; Abb. 91 (nervation diagram).

p 1983 Alethopteris valida Boulay; Josten, 132, Abb. 95; Taf. 48, figs 2, 2a; non Taf. 48, figs 1, 1a (= Alethopteris valida Boulay, 1876).

p 1984 Alethopteris lonchitius (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 davreusi); 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 lonchitius (Schlotheim); Delvolvé & Laveine, 293-294, pl. A, fig. 2, pl. 6, fig. 4.

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

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

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

1991 Alethopteris lonchitius (Schlotheim) Sternberg; Josten, 291-293, Taf. 158, figs 1, 1a, 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).
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) Zeiller; Kota- sowa in Dybová-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 Šusta, 1928: Taf. XXXIV, fig. 3), fig. 6 (trichome); pl. XI, 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 7-9 (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, Coquel, Mercier & Sartori, Pl. III, figs 2, 3 (together with *Neuralethopteris schlehanii*), fig. 4 [with *Paripetites 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 lonchitides* 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).


1905 *Alethopteris lonchitica* Schlotheim; Vinassa de Regny & Gortani, 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 & Pfeifferkorn, 1986, is synonymous with *Alethopteris virginiana*).

1908 *Alethopteris lonchitica* Schlotheim; Renier, 37, fig. 12 (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. LXXXIX, 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-westphalenis* 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-
pteroides – Jongmans already expressed some doubt, mentioning a possible confusion with Neuroleptopteris schlehanii).

1957 Alethopteris lonchitica Brongniart (sic); Kindelán, 99, fig. 4-4 (fragmentary specimen, difficult to judge, but clearly not Alethopteris urophylla).

1958 Alethopteris lonchitica Schlotheim; Langford, 241, Figs 438, 439 (also mentioned in Leary, 1976) (to be compared with Alethopteris lesquerellii).

1962 Alethopteris lonchitica (Schlotheim) Göppert; Migier, 85, 89, Tab. VIII, figs 1-2 (difficult to judge from the illustration; probably indeterminable).

1967 Alethopteris lonchitica (Schlotheim) Zeiller (sic); Migier, 85, 89, Tab. VIII, figs 1-2 (difficult to judge from the illustration; probably indeterminable).

1966 Alethopteris lonchitica (Schlotheim) Zeiller (sic); Migier, 85, 89, Tab. VIII, figs 1-2 (difficult to judge from the illustration; probably indeterminable).

1970 Alethopteris lonchitica (Schlotheim) f. selii (Brongniart) Gothan; Havlena, pl. I, fig. 13; Pl. II, fig. 5 (only one specimen which is assigned to Alethopteris havlennae by Šimůnek, 1996: 10).

1972a Alethopteris lonchitica Schlotheim; Bitoianu, pl. II, fig. 13 (= Alethopteris cf. davreuxii).

1972b Alethopteris lonchitica Schlotheim; Bitoianu, pl. IV, fig. 3 (= too fragmentary, possibly Neuroleptopteris).

1973 Alethopteris lonchitica Zeiller (sic); Bitoianu, pl. III, fig. 29 (to be compared with Alethopteris westphalensis).

1972c Alethopteris lonchitica (Schlotheim) Schlotheim; Caride, Greber & Ortuño, pl. II, figs 1, 1a; pl. III, figs 3, 3a [to be compared with Alethopteris westphalensis and Alethopteris missouriensis, and probably the same species as that recorded (erroneously) as Alethopteris decurrens by Caride et al., 1973: pl. II, figs 2-3].

1977 Alethopteris lonchitica (Schlotheim) Sternberg; Leary & Pfefferkorn, 25-27, text-fig. 9A-D, pl. 9, figs 1-6 (specimens previously mentioned in Leary, 1976: 4) (to be compared with Alethopteris havlennae).

1978 Alethopteris lonchitica; Gillespie, Clendening & Pfefferkorn, 100, pl. 35, fig. 3 (nervation diagram); pl. 36, fig. 7 (pointed pinnules tending to a lanceolate shape not suggestive of Alethopteris urophylla).

1997 Alethopteris lonchitica (Schlotheim) Göppert; Anisimova, Tab. XXXIV, fig. 4 (= Alethopteris decurrens).

1982 Alethopteris lonchitica (Schlotheim) Brongniart; Oleksysyn, 98-99, figs 19F-H (to be compared with Alethopteris missouriensis).

1985 Alethopteris cf. lonchitica (Schlotheim) Brongniart; Lyons et al., pl. XI, fig. b (very fragmentary; either Neuroleptopteris sp. indet. or Alethopteris sp. indet.).

1986 Alethopteris lonchitica (Schlotheim) Purkyňová, Tab. IV, fig. 3 (= Alethopteris havlennae) (Šimůnek, 1996: 14, includes this specimen in Alethopteris urophylla).

2000 Alethopteris cf. lonchitica; Laveine et al., 506-507, pl. X, figs 1-2 (probably to be compared with Neuroleptopteris obliqua sensu lato).

? 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; Němec, 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 tripinnati-fidis; pinnis primaris apice tantum pinnatifidis, pinnulis linearibus longissimis decurrentibus; inferiis bipinnatifidis pinnulis elongatis, in pinnulam linearem maximam desinentibus; pinnulis lateralis subs conformibus, in pinnis infe-rioribus majoribus, obliquis, oblongis, obustisculis, sub contibus, basi paulum dilatatis, decurrentibus et connatis, integerrimis, lineâ impressâ marginatis; nervio medio angusto approximato, nervulis tenuissimis simplicibus vel plurumque furcatis vix obiquis”.

This translates as follows: Tripinnate frond; terminal of primary pinnae clearly pinnatifid, pinnules long, linear and decurrent; lower bipinnate pinnules 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).

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. 60-80º angle, very narrowly confluent, slightly asymmetrical, with a sloping base and a marked constriction on the acroscopic side. Last order pinnule 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
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 triipinnate) 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:** *Alethopteris 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 Buisine, 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 *Alethopteris decurrens* pinnales seem more irregular than those of *Alethopteris urophylla*. However, certain parts of *Alethopteris urophylla*, which are characterised by more elongate pinnules, may resemble *Alethopteris decurrens* (hence the doubts attached to the drawing of *Alethopteris heterophylla*). Kidston (1886: 134) observed gradual transitions between *Alethopteris decurrens* and *Alethopteris lonchitica* (auctorum), and Crookall (1955) noted their similar stratigraphic range. The species introduced by Stockmans & Willière (1952–53) as *Alethopteris edwardsii* (1953: 240; 1952: pl. LVI, figs 9, 9a) and *Alethopteris 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 *Alethopteris 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.

*Alethopteris 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 *Alethopteris urophylla*. Vein density of 45–50 veins/cm is similar to that of *Alethopteris urophylla*. It may be that *Alethopteris lancifolia* should be regarded as an extreme form of *Alethopteris 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 *Alethopteris urophylla*. N.B. Two of the specimens figured as co-types of *Alethopteris lancifolia* by Wagner (1961: pl. 2, figs 6–7) should be excluded because of pinnule shape, the much wider confluence between pinnales, and a wider venation. A comparison with *Alethopteris valida* is suggested. No revision of *Alethopteris lancifolia* is attempted here, but compare Wagner (2005).

*Alethopteris hermetetii* Buisine (1961: 115–125, pls XXI–XXVI) shows pinnules similar in shape and size to those of *Alethopteris urophylla*. However, pinnule insertion seems on the whole more perpendicular and the constriction on the acroscopic 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 Buisine (1961: 116), the vein density is c. 30 veins per cm, which is less than that admitted for *Alethopteris urophylla*.

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

*Alethopteris lonchitica* Schlotheim ex Sternberg has pinnales 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 pinna. Its lateral veins are more widely spaced. The pinnales of *Alethopteris lonchitica* tend to be more pectopteroid, and more nearly perpendicular to the rachis. *Alethopteris friedelii* (= *Alethopteris ambigua*) is a synonym of *Alethopteris lonchitica*. This is an upper Westphalian species which ranges into basal Stephanian.

The Bolsovian species *Alethopteris bertrandii* Bouroz, 1956 possesses stiff, almost parallel-sided pinnales, 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

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**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 where 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 Valdevaria 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 Bronniart (1834), is the same as most specimens recorded as Alethopteris lonchitica in the literature, i.e. Alethopteris lonchitica (auctorum). In fact, Bronniart’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 Bronniart (1833). The specimens illustrated by Bronniart (1833: pls 84, 128) are apparently from three different localities, viz. Dudweiler near Saarbrücken, the vicinity of Namur in Belgium, and Newcastle-on-Tyne in northeast England. Bronniart (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 Bronniart, 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 Neuraletheopteris neuropteroides (Šusta, 1927) Josten, 1983. Additional remains (pl. 84, figs 4, 5, 6) might well belong to the same species, thus leaving only Bronniart’s pl. 84, figs 1, 1a as Alethopteris lonchitica (auctorum). It is not immediately obvious how Bronniart 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 Bronniart’s Alethopteris lonchitica of his plate 84, figs 1, 1a, and the holotype of Alethopteris urophylla do share this character to a marked degree. Bronniart was most interested in comparing with the morphological characters of certain Recent ferns, and referred more particularly to Pteris. After diagnosing “Pecopteris” urophylla (Bronniart, 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 Bronniart’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 Bronniart’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 Bronniart’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. Bronniart’s drawing shows both once forked and simple veins, which accords rather well with his statement (Bronniart, 1834: 290) of both simple and bifurcate (and even more than once bifurcate) veins in Alethopteris urophylla. Bronniart’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. Bronniart’s pl. 128 shows a possibly different species which Buisine (1961) identified with Alethopteris friedelii. 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

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**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 open cast 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 nervules, 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 (Bolsovian) 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 acroscopic 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 *Alethopteris urophylla*. This opinion is not maintained by the present writers, who prefer to assign this specimen to *Alethopteris westphalensis*. The specimen in question shows pinnules which are less constricted on the acroscopic side than is customary for *Alethopteris urophylla*.

Buisine (1961: 89) compared with *Alethopteris lonchitica* (auctorum) in the sense of Zeiller (1886-88), separating his *Alethopteris serlii* (i.e. *Alethopteris densinervosa* and *Alethopteris westphalensis*) from *Alethopteris lonchitica* (auctorum) (i.e. *Alethopteris urophylla*), as occurring in northern France, primarily on stratigraphic criteria. However, Buisine also drew attention to the more asymmetrical aspect of the pinnules of *Alethopteris 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 *Alethopteris lonchitica* (auctorum), with respect to localities in the British Isles. He included in the synonymy both *Alethopteris urophylla* and *Alethopteris 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 *Alethopteris 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 *Alethopteris 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 *Alethopteris lancifolia* 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 *Alethopteris lonchitica*. Both are fairly typical of *Alethopteris urophylla* in general morphology, and vein density (45-55 veins/cm). These specimens came from Langsettian and Duckmantian strata.

Wagner (1953) recorded *Alethopteris lonchitica* from the same West German area as dealt with by Josten (1991). He illustrated several different forms; a number of specimens (Wagner, 1953: Taf. 4, figs 2, 3, 5; Taf. 5, figs 1, 4, 5; Taf. 6, figs 2-4) conform to *Alethopteris urophylla* (= *Alethopteris lonchitica* sensu Zeiller, as figured later by Josten, 1991), whereas another (Taf. 4, fig. 1) has been ascribed by Wagner (1961) to his *Alethopteris lancifolia*. Two additional remains, from the middle Namurian (Taf. 4, fig. 3) and the Bolsovian (Taf. 4, fig. 4), respectively, are tentatively attributed to *Alethopteris lancifolia* and *Alethopteris westphalensis*. Gothen (1953: Taf. 5, fig. 3) also figured as *Alethopteris lonchitica* (forma serlii) a specimen which is very different, and comparable to *Alethopteris grandinioides* Kessler according to Wagner, 1968 (referred to *Alethopteris pseudograndinioides* by Zodrow & Cleal, 1998). A specimen figured by Franke (1912) as *Alethopteris serlii* forma platyrachis (only a drawing), was illustrated photographically by Gothen (1953: Taf. 6, fig. 1), as *Alethopteris lonchitica* forma serli. This specimen was attributed, with doubt, to *Alethopteris westphalensis* by Wagner (1968), who commented on this specimen in detail. It may be more properly ascribed to *Alethopteris havlenaee*.

*Alethopteris vulgator* Sternberg, 1825, which is commonly attributed to *Alethopteris 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 *Neuralethopteris neuropteroides*, rather than *Alethopteris lonchitica* (auctorum). It is here rejected as a possible synonym of *Alethopteris urophylla*. *Alethopteris vulgator* was renamed *Alethopteris 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 *Alethopteris lonchitica* (pars); these specimens are attributed by the present writers to *Neuralethopteris neuropteroides*. Ettingshausen (1854) figured as *Alethopteris sternbergii* a specimen which Wagner (1968) referred to *Alethopteris missouriensis*. This species is quite different from *Alethopteris vulgator* (= *Neuralethopteris neuropteroides*?).

Although not directly relevant to the synonymy of *Alethopteris urophylla*, the species “Neopteris” *distans* Sternberg, 1825, *nomen nudum*, but figured as *Alethopteris lonchitifolia* by Kvaček & Kvaček (1992), and Kvaček & Štraková (1997), might belong to either *Alethopteris lonchitifolia* or *Alethopteris 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 pinna 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 Pennsylvanian 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 predominantly 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-
ope (Wagner, 2004). 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

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**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 hele nae* Lesquereux, 1879. This is undoubtedly 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

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**Figure 13.** Chart depicting stratigraphic ranges established for the different areas in the palaeoquatorial belt where records of *Alethopteris urophylla* exist.
Alethopteris 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 Alethopteris urophylla to range from basal Langsettian to about mid-Bolsovian. Arber (1914) and Crookall (1955) mention Alethopteris 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 Alethopteris urophylla from Nord/ Pas-de-Calais are mainly under the name of Alethopteris lonchitica (Buïsine, 1961), but it seems that some remains identified as Alethopteris serlii also belong to Alethopteris urophylla (compare list of synonymy). The ranges given by Buïsine (op. cit.) show Alethopteris lonchitica (auctorum) as mainly occurring in Langsettian and lowermost Duckmantian, with a total range from Yeadonian to upper Duckmantian. The specimen figured by Buïsine (1961: pl. VIII, figs 2, 2a) as Alethopteris serlii, but attributed by the present authors to Alethopteris urophylla, originated from the Faisceau d’Ernestine, Assise de Bruay, lower Bolsovian.

In Belgium, which continues the area of coal-measures in northwestern France, Alethopteris 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 Alethopteris 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 Alethopteris 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-
Alethopteris lonchitica (auctorum)

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 the Sydney Basin in 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 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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