SPHENOPTERIS HADROPHYLLA KNIGHT MS, A POSSIBLE DISCOPTERIS, FROM THE UPPER STEPHANIAN OF NW SPAIN

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Knight, J.A. & Wagner, R.H. (2012). *Sphenopteris hadrophylla* Knight MS, a possible *Discopteris*, from the upper Stephanian of NW Spain. [*Sphenopteris hadrophylla* Knight MS, un posible *Discopteris* del Estefaniense superior del NO de España]. *Revista Española de Paleontología*, **27** (1), 45-66. ISSN 0213-6937.

ABSTRACT

The upper Stephanian fern *Sphenopteris hadrophylla* Knight, described originally in an unpublished thesis on the Sabero Coalfield in León, NW Spain, is now validly introduced on the basis of new, more complete, material collected from the La Magdalena Coalfield in León. This includes sporangiate pinnae interpreted as possibly attributable to *Discopteris* Stur. A holotype and paratypes are designated from this material. The more fragmentary specimens from Sabero are recorded also. Additional specimens from Villablino (León), El Bierzo (León), Ciñera-Matallana (León), and the Narragansett Basin in New England (U.S.A.) are referred to and partly illustrated, thus demonstrating the wider distribution of the species. Comparisons are made with several species of Stephanian age known from Europe and North America.

Keywords: Fern foliage, *Sphenopteris*, *Discopteris*, Stephanian, NW Spain.

RESUMEN

El helecho estefaniense *Sphenopteris hadrophylla* Knight, que fue descrito originalmente en una tesis inédita sobre la cuenca minera de Sabero (León), se introduce aquí formalmente en base a un material más completo obtenido de La Magdalena (León), que incluye pinnas esporangiadas, posiblemente atribuíbles a *Discopteris* Stur. Se designan el holotipo y los paratipos de este material, haciendo mención también a los ejemplares, más fragmentarios, descritos originalmente de Sabero. Registros adicionales procedentes de Villablino (León), El Bierzo (León), Ciñera-Matallana (León), y de la cuenca de Narragansett, EE.UU., demuestran la amplia distribución de la especie. Se compara con varias especies diferentes del Estefaniense europeo y de los Estados Unidos.

Palabras clave: Helechos, *Sphenopteris*, *Discopteris*, Estefaniense, NO de España.

INTRODUCTION

The fl oral remains from Sabero (northern León), one of the post-Asturian coalfi elds that follow the definitive outline of the arcuate fold belt in the Cantabrian Mountains (Figs 1, 2), have been recorded in an unpublished Ph.D. thesis (Knight, 1975). Although a substantial part of the upper Barruelian-Saberian (mid-Stephanian) floras from Sabero has been published subsequently (Knight, 1983b, 1985), the sphenopterids are not yet dealt with in publication. This means that some new species, such as *Sphenopteris hadrophylla* Knight, 1975, were not yet validly introduced in the literature, even though the names have been used occasionally. Indeed, material identified as *Sphenopteris hadrophylla* has been illustrated from La Magdalena (León) by Castro (2005, lám. 15). Since the specimens used for the original description were rather fragmentary, the opportunity is taken here to designate a holotype and paratypes on more recently collected, more complete material found in the La Magdalena Coalfield, another post-Asturian outlier in the province of León (Fig. 2). This includes fertile pinnae of uncertain attribution.

It is noted that this coalfield and the intervening area of Ciñera-Matallana are tectonic outliers which form part

https://doi.org/10.7203/sjp.27.1.18096

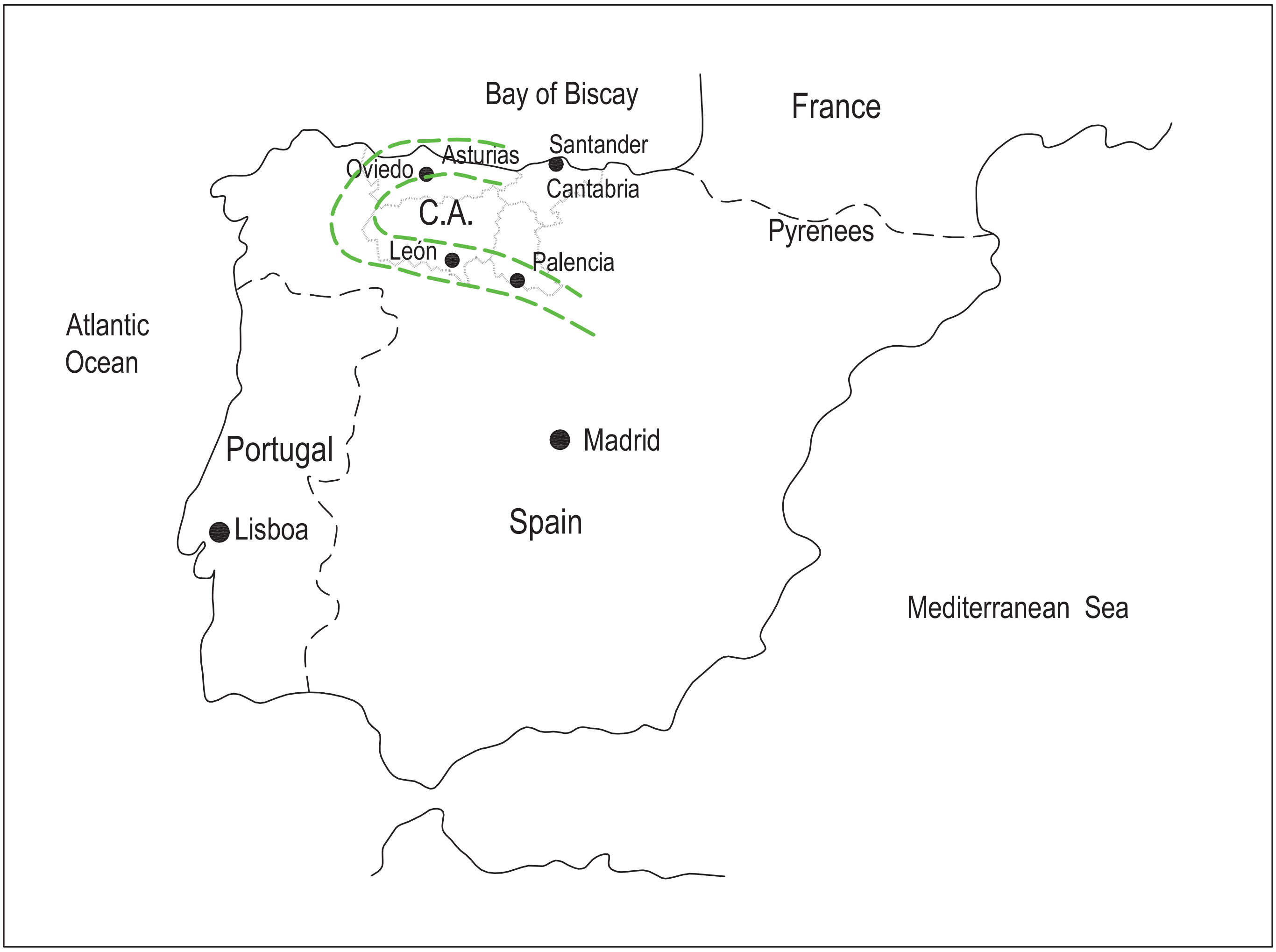

Figure 1. Map showing the position of the Cantabric-Asturian arcuate fold belt (C.A.) in the Cantabrian Mountains, NW Spain (after Wagner & Castro, 2011).

of the same basin of sedimentation as Sabero (Figs 2, 3). Westerly onlap has been recorded within both the Sabero and Ciñera-Matallana coalfields, and a correlation based on the angle of onlap and a major lacustrine flooding event recorded from both coalfields has recently been proposed by Wagner & Castro (2011, Fig. 4). Formations as recognised in these coalfields by Wagner (1971) and Knight (1983a) are placed in their relative position in Fig. 3. Using the same onlap criteria, this correlation has been extended westwards into the La Magdalena and Villablino outliers (Fig. 3). The latter is shown with separate columns for its eastern part at Carrasconte and the main coalfield area of Villablino. The initial post-Asturian basin lay in the eastern part of the Sabero area (Iwaniw & Knight, 1981). Its gradual expansion westwards is accompanied by abundant evidence of a mobile basin margin adjoining a rugged palaeotopography, which is emphasised by the presence of deeply incised E-W striking palaeovalleys as recorded by Wagner *in* Wagner & Artieda (1970), Heward (1978) and Wagner & Castro (2011). Evidence for a substantial palaeotopography in the area of Villablino was described by Corrales & Peláez-Pruneda (1968).

The records of *Sphenopteris hadrophylla* Knight in the Sabero, Ciñera-Matallana and La Magdalena coalfields are all from the Saberian Substage as introduced by Wagner & Álvarez-Vázquez (2010a). A lower Stephanian B position is indicated for specimens illustrated from the Villablino Coalfield (León) by Álvarez-Ramis (1965 – see list of synonymy below). Additional specimens from El Bierzo (also in northern León – Fig. 2) are less precisely located in the overall stratigraphic succession, but might be from basal Stephanian B.

The description of *Sphenopteris hadrophylla* as given in the following pages is based primarily on the material recovered from the La Luisa opencast mine which worked the lowermost part of the succession at La Magdalena (Interval 1 of Wagner & Castro, 2011), and which yielded a large collection of floral remains. These include the types as designated in the present paper.

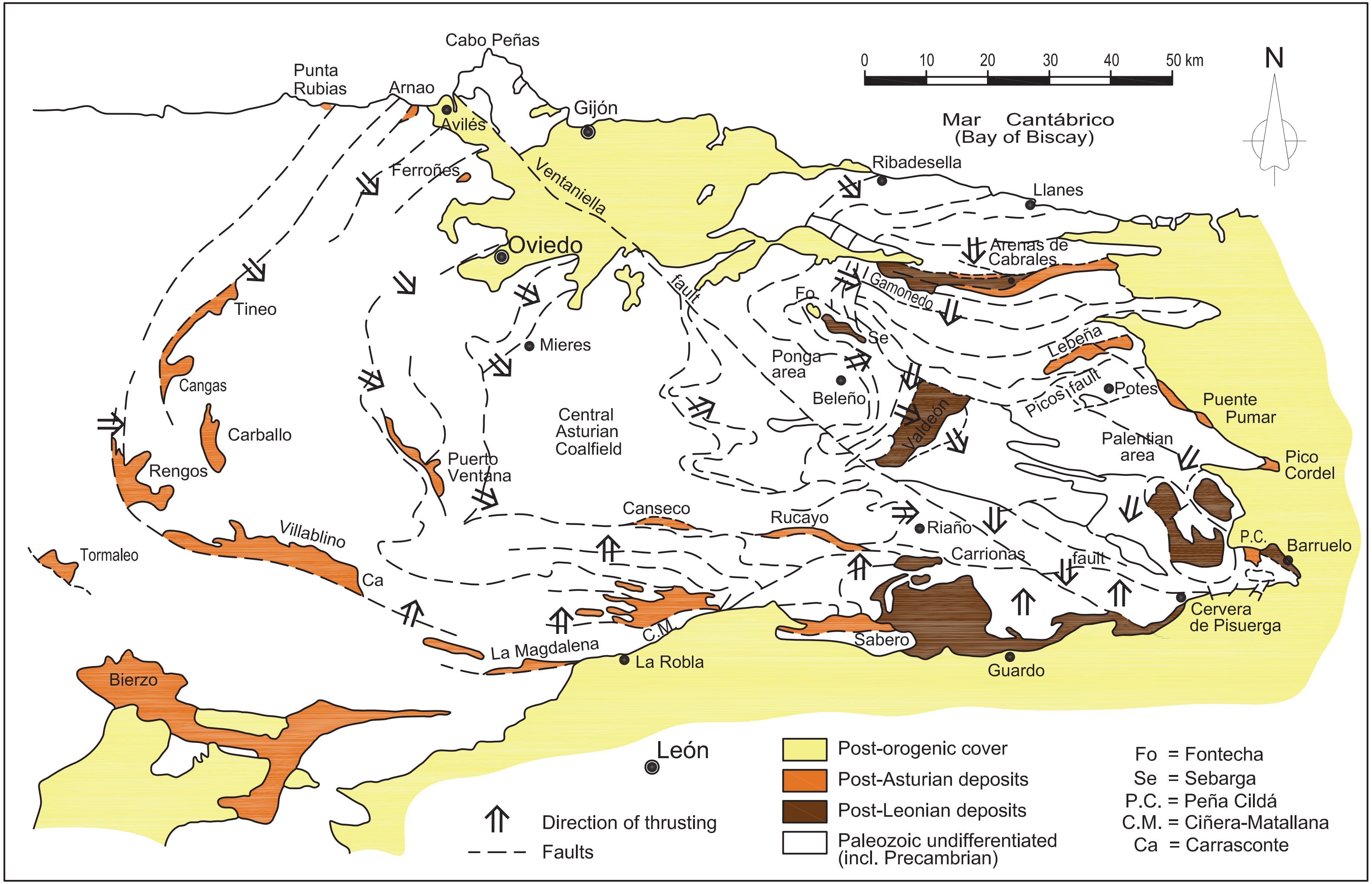

Figure 2. Map showing the outcrop pattern of post-Asturian coalfields (upper Barruelian, Saberian, Stephanian B *sensu* St. Étienne) in the Cantabrian Mountains, NW Spain (after Wagner & Castro, 2011).

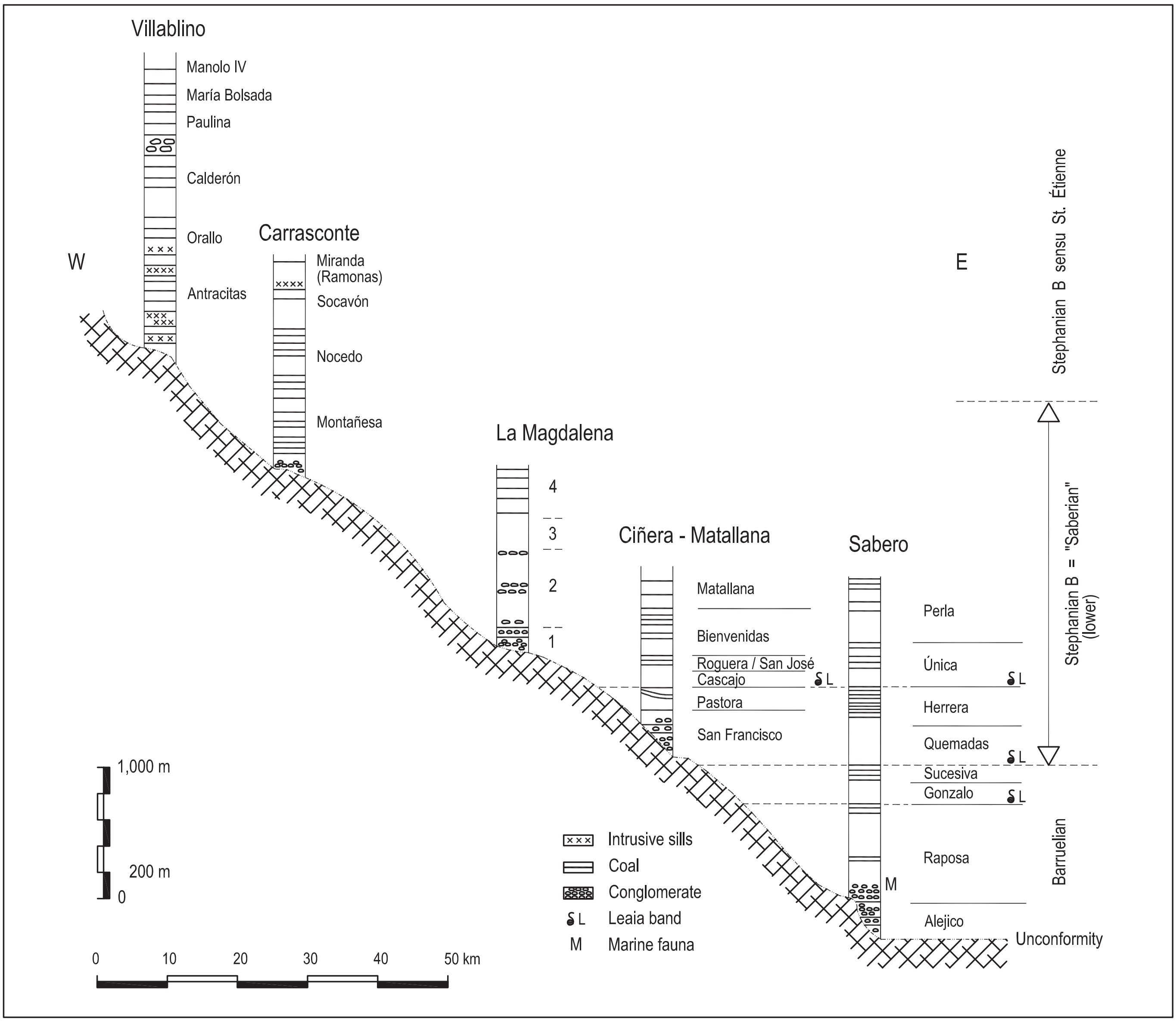

Figure 3. Generalised stratigraphic columns showing the correlation between the successions in the Sabero, Ciñera-Matallana, La Magdalena and Villablino (including Carrasconte) coalfield areas, representing westerly onlap in a single (coastal) basin of sedimentation (after Wagner & Castro, 2011). All coalfields in northern León province (compare Fig. 2).

SYSTEMATIC DESCRIPTION

Filicophyta *incertae sedis*

Genus *Sphenopteris sensu lato* Brongniart, 1828

Remarks: Usage of the term *Sphenopteris* is lax, and refers to incised, lobate pinnules with constricted bases. Both fern and pteridosperm foliage has been described under this general denomination. Van Amerom (1975) has pointed out that the type species, *Sphenopteris elegans* (Brongniart) Sternberg (same as *Filicites adiantoides* Schlotheim), is a pteridosperm, and is currently recorded under *Eusphenopteris* Simson-Scharold (for a full discussion and photographic illustration of the type specimen of *Sphenopteris elegans*, see van Amerom, 1975).

Fern foliage falling under the general heading *Sphenopteris* is described preferably as belonging to one of the more closely circumscribed genera based on fertile material. The different sporangiate organisations are quite distinctive, and where adequately preserved fertile material is available, the different sphenopterid fern species are ascribed to one of these genera (for a full discussion see Brousmiche, 1983). However, where sphenopterid fernlike foliage is recorded without benefit of attached fertile material, the term *Sphenopteris* is used for expediency, even though there is full awareness of the lack of precision that this implies. In the present paper a sphenopterid fern is described which shows attached fertile pinnae demonstrating that a true fern is being dealt with. However, a relatively coarse grain size prevents the adequate detail to be observed for a precise generic attribution.

The development stages of pinnule growth in *Sphenopteris* species and the progress of lobing to attain the pinna stage were analysed by Danzé (1955a) and found to be diagnostic features for species identification based on vegetative foliage. Of importance is the differentiation between apical and equilateral growth of pinnules as these approach the transition to pinnae (Danzé, 1955a). The "critical" number was defined (Danzé, 1956, p. 133) as the number of pairs of lobes at the stage where the basal pair of lobes become fully incised and the lobed pinnule completes the transition to a small pinna.

Sphenopteris hadrophylla Knight MS, 1975
Figs 4a-13c

v 1964 *Sphenopteris weissi*; Wagner, p. 841.
1965 *Sphenopteris lebachensis*; Álvarez Ramis, p. 24-25, lám. XII, Figs 1, 1a-c.
1965 *Sphenopteris* aff. *weissi*; Álvarez Ramis, p. 39-40, textfig. 27, lám. XXI, Figs 2-3a.
1967 *Sphenopteris lebachensis*; Álvarez Ramis, p. 129-130, textfig. 105, lám. XII, Figs 1, 1a-c (same plate as in Álvarez Ramis 1965).
1967 *Sphenopteris* aff. *weissi*; Álvarez Ramis, p. 146-147, textfig. 115, lám. XXI, Figs 2-3a (same plate as in Álvarez Ramis 1965).
v 1975 *Sphenopteris hadrophylla* Knight, p. 295-302, pl. 21, Figs 1-4a.
1978 *Sphenopteris minutisecta*; Lyons & Darrah, p. 435, Fig. 3H-J (cf. *hadrophylla* according to Wagner & Lyons, 1997, p. 279).
1997 *Sphenopteris* cf. *hadrophylla*; Wagner & Lyons, p. 279 (with reference to Lyons & Darrah, 1978).
v 2003 *Sphenopteris hadrophylla*; Castro, t. 1: p. 90, 103, 154; t. 3: lám. 5, Figs 1-3, lám. 6, Figs 2-6.
v 2005 *Sphenopteris hadrophylla*; Castro, t. I: p. 50, 78, lám. 15, Figs 1-3 (same as Castro, 2003, lám. 5, Figs 1-3).
v 2010a *Sphenopteris hadrophylla* (*nomen nudum*); Wagner & Álvarez-Vázquez, p. 282, 283, 312, Tables 7, 8.
v 2011 *Sphenopteris hadrophylla*; Wagner & Castro, p. 52.

Derivatio nominis: The name describes the characteristic thick-limbed appearance of the species; *hadros* (Greek) – thick; *phyllon* (Greek) – leaf.

Material: A number of well preserved fragments of pinnae have been collected from the tip of the La Luisa opencast mine in the La Magdalena Coalfield (RHW loc. 4298), in the province of León. These are all adpressions. A holotype and several paratypes have been selected from this material which shows the limited range of variation in the characteristically coriaceous pinnules, showing apical growth. The apparent absence of aphleboid pinnae is noted. Pinnae of the antepenultimate and an even higher order are available from the type locality. Some pinnae are entirely or partially fertile. Additional remains of a more fragmentary nature have been collected from the Sabero, Ciñera-Matallana, and Villablino coalfields, and from El Bierzo, all in the province of León (see list of localities).

Type material: The specimen figured as Figs 4a-b is designated the holotype from the type locality RHW loc. 4298 of La Magdalena coalfield. Paratypes are figured as Fig. 4c, Figs 5a-b, Fig. 6, Figs 7a-e, Figs 8a-b, Fig. 10 and Fig. 11.

Material which formed the basis of the informal first identification (Knight, 1975) from the Sabero coalfield and Ciñera-Matallana coalfield, respectively, is illustrated as Figs 13a-b.

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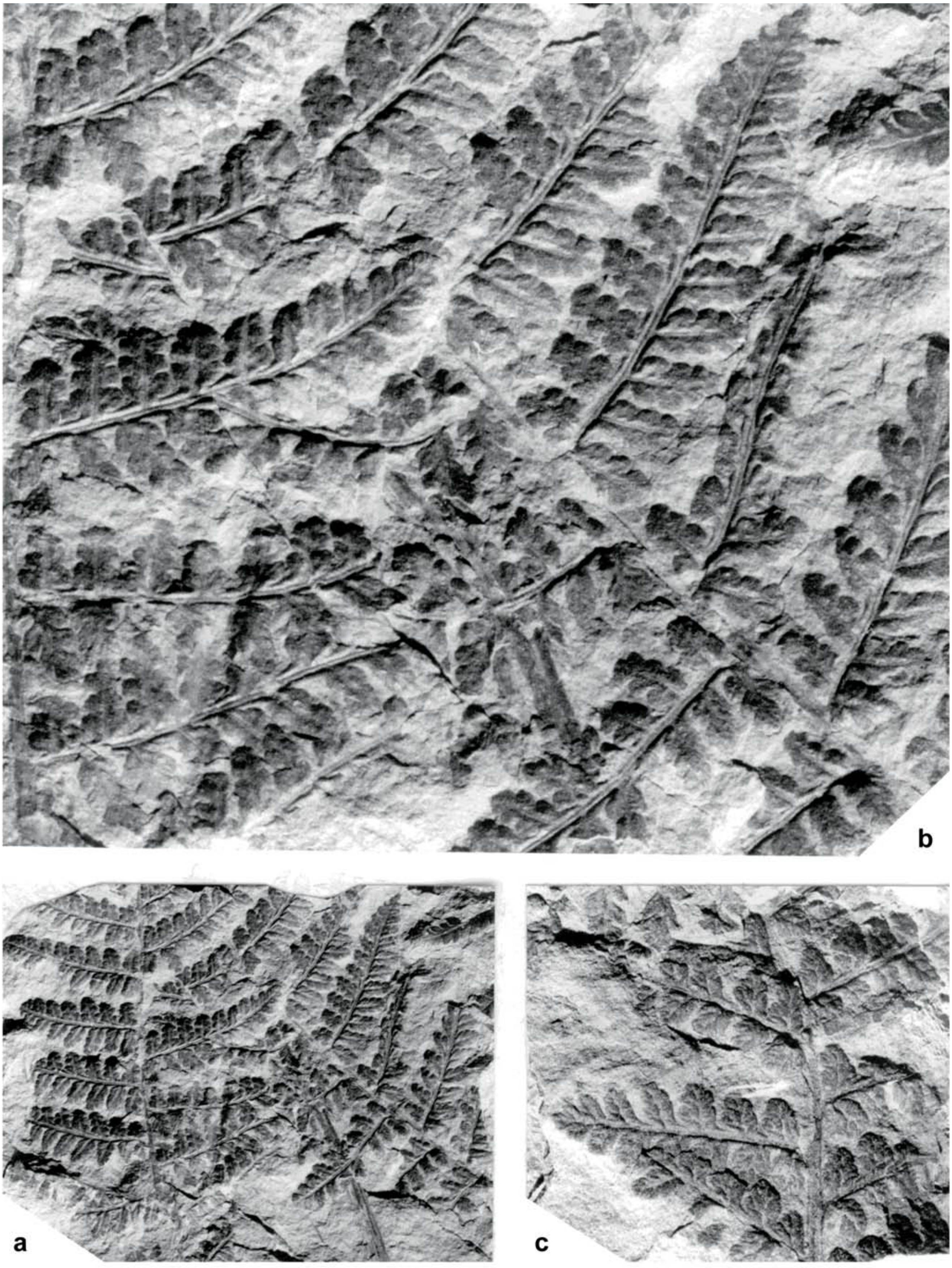
Diagnosis: At least quadripinnate fronds with perpendicularly inserted pinnae characterised by robust pinnules. Pinnae relatively small, elongate and gradually tapering, with robust rachises. Last order pinnae (7-30 mm) parallel-sided and tapering abruptly in the terminal which shows a small, blunt apical pinnule. Basal catadromous pinnae of penultimate order broadly triangular and spreading. Last order rachises robust and flanged. Pinnules (1-7 mm long) robust, oblong and squat with a thick, convex lamina and undulating margins. Blunt, weakly incised lobes very widely inserted. Lobing very gradually developed; pinnule development of slow apical type. Pinnule lobes become fully incised at the pinna stage (length/breadth = 2.5:1) when five pairs of lobes are developed (critical number of 5). Venation is robust, with a straight, strong midrib extending into near the pinnule apex. A single lateral vein enters each lobe. Fertile elements show sori corresponding to pinnule lobes.

Description: *Organisation of the frond.* The most complete specimen with regard to frond organisation is an antepenultimate order pinna (upper part illustrated as Figs 5a-b and Fig. 6) of over 180 mm length and width up to 75 mm. The antepenultimate order rachis arises perpendicularly from a robust lower order rachis of width 4 mm with dense fine punctate markings. The


b
a
c

antepenultimate order rachis is 3 mm wide and also punctate. This specimen is incompletely figured and is quadripinnate; as is that in Fig. 8. A tentative reconstruction indicates a minimum frond width of 600 mm.

Pinnae of the penultimate order are alternately inserted at a wide angle, not quite perpendicular, and are frequently flexured forward. Length at least 70 mm, very gradually tapering, up to 30 mm wide at the base; well spaced and generally not touching laterally. Terminal acute, with a small apical pinnule. Basal pinnae of the last order appear slightly turned away from the next adjacent pinna and tend to align close to the higher order rachis.

Rachis of the penultimate order fairly robust, 0.7-1 mm wide, generally straight but slightly flexuous near the terminal; striate with a narrow flange.

Pinnae of the last order inserted alternately, at a very wide angle, almost perpendicularly, and of robust appearance. Sides subparallel but tapering rather abruptly in the terminal part of pinnae, which are topped by a very small, lobate, apical pinnule. The transition from lobate pinnule to last order pinna is attained at a length of 7-9 mm. Longest last order pinnae are 30 mm, at a basal width of 12 mm. Length-breadth (l/b) ratios are normally about 3:1, but occasionally as low as 2:1. Basal catadromous pinnae upon the penultimate order pinna are characteristically squat and broad, l/b ratio approaching 1.5:1. Their shape is broadly triangular, and they are more spreading than standard pinnae. The basal catadromous pinnae tend to extend parallel to the main rachis. However, they do not show any marked reduction of pinnule lamina and are therefore not aphleboid.

Rachis of the last order straight and quite robust (0.3 mm), generally flanged as a result of narrow fusion of pinnule bases.

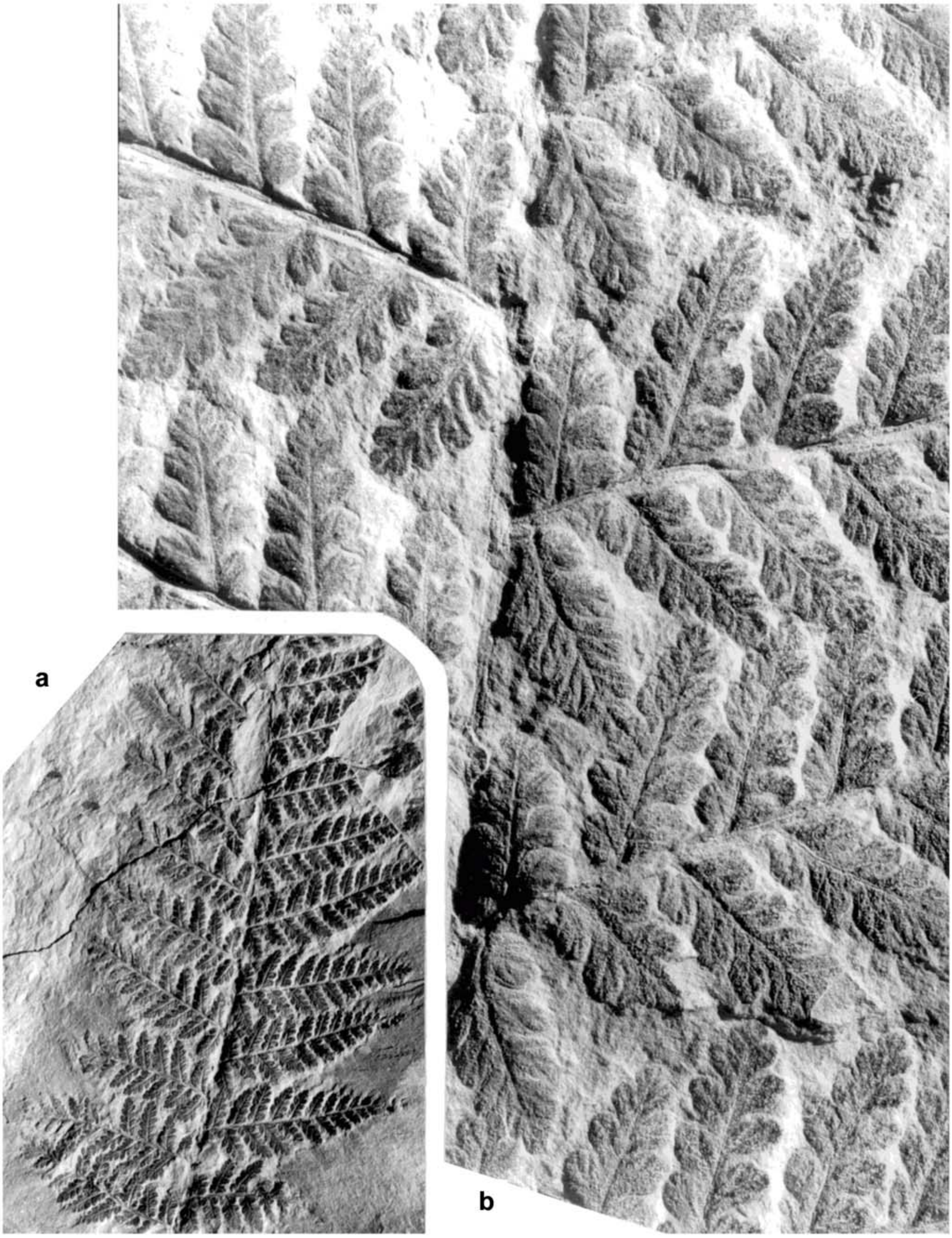
Pinnules very robust, squat, with a vaulted lamina; they are inserted at a very wide angle, which becomes a right angle in the longer pinnae. Shortest pinnules (1 mm long) are of blunt oblong appearance and fully attached across the basal width. Decurrent pinnule bases fuse to produce a flanged rachis. Margin irregular, lobate to undulate. Lobing is gradual, the lobes being rounded and separated by shallow sinuses. Gradual narrowing of the base progresses with lobe incision, which is sigmoidal. The pinna stage is attained at a pinnule length of c. 7 mm at l/b ratio 2:1. At this stage there are five sets of slightly angular lobes, separated by incisions higher up. The pinnule lamina is convex, leathery in appearance, with deeply imbedded veins which are generally rather indistinct beyond the midrib.

Pinnule development. On attaining the pinna stage, the individual lobes (pinnules) are of oblong shape with one set of weak indentations near the apex, with an l/b ratio approximately 1:1 or slightly greater in near-terminal areas. Increase in pinnule size is equilateral to the stage where the indentations originally at the top become developed as distinct lobes halfway up the pinnule. At this stage a second set of indentations is developed also near the top, maintaining the blunt appearance. Subsequently, there is a gradual elongation to an l/b ratio of about 1.5:1, which is maintained up to the development of the fourth lobe. The pinnule attains the pinna stage when five sets of lobes are developed (Fig. 9), a critical number of 5 (after the definition in Danzé, 1956, p. 133), and at this stage the l/b ratio is 2.5:1 and the shape has become narrowly triangular. From this stage elongation of the pinna continues gradually and can attain an l/b ratio of 3:1. This is an example of slow apical development, the growth consisting of a very gradual, but consistent elongation of pinnules (see Danzé, 1955a).

Venation. Midrib strongly marked, straight and occasionally very slightly decurrent, and remaining well-marked to near the pinnule apex. Robust lateral veins arise at an angle of c. 40º, each lateral entering a lobe in which it extends to the top. Lateral veins are rarely seen to bifurcate. Veins deeply imbedded in the pinnule lamina, to which they give a furrowed appearance; this often emphasises the uneven margins. The deeply imbedded nature of the veins generally impedes the observation of venation detail.

Sori. Fertile pinnae occur in the apical area of penultimate order pinnae (Fig. 10), in which there is a clear transition from vegetative pinnae, through pinnae with mixed vegetative and fertile foliage to entirely fertile. The development of fertile areas is marked firstly by the appearance of oval impressions, still poorly defined, in the first or lowermost occurrences, and representing apparent groupings of sporangia (sori) in the near-terminal part of last-order pinnae. The lack of clear definition is due to the tendency for fertile pinnules to become infolded with apparent retraction of the pinnule lamina around the sori, and also to the relatively coarse grain size of the silty host sediment which obscures detail at the level of individual sporangia. In available material no more than two successive last order pinnules show mixed vegetative and fertile material before the development of entirely fertile pinnae. Up to five successive fertile pinnae are seen to occur in the apical part of penultimate order pinnae. Partly fertile pinnae show that the development of fertile pinnules is marked by a twisting of the pinnule surface to become more horizontal, such that the fertile areas are somewhat buried in the sediment whereas vegetative pinnules are relatively flatter.

Figure 4. a) Holotype, x 1. Two partially superimposed pinnae of the penultimate order. **b)** Holotype, x 3. Partial enlargement. **c)** Paratype, x 3. Fragment of a pinna of the penultimate order showing pinnae with small, quintulobate pinnules. RHW loc. 4298, La Magdalena.


a
b

Sori in the developmental stage on existing pinnule lamina are of oval shape with a maximum long-axis dimension of no greater than 0.9 mm. Sori appear as isolated organs initially close to the margin, but within the pinnule lamina. In the more distal parts of fertile pinnae the sori become more clustered and overlap the pinnule margins. The sori commonly show undulate margins which reflect an internal segmented structure apparently indicating the grouping of sporangia in a synangial structure which cannot be described in detail because of poor preservation.

Entirely fertile pinnae show a stiff, stalked structure in which the pinnules on last order pinnae are reduced to a flanged thick pedicel with clusters of sori, associated with indistinct veins and ribbons of retracted pinnule lamina, although in some cases appearing to be pendant on stalks representing modified pinnule veins. The fertile pinnae are inserted almost perpendicularly on the last order rachises.

Although the sori cannot be interpreted definitively, where identified as deep depressions on pinnule lamina up to eight individual segments seem to occur as a radial cluster around a central attachment (Fig. 11). Where fertile pinnules are reduced to apparently stalked clusters of sporangia, these occasionally show a radiating but conjoined stellate structure, with 5-7 elements.

Attribution of sori: The available material illustrates the size, shape and progressive development of sori, but poor preservation does not allow a clear identification of sporangia within the sori. By comparison with the range of published material of the genus *Discopteris* Stur, and also by comparison with the robust vegetative foliage associated with this genus, the closest comparison of the present fertile material is with *Discopteris*.This genus was introduced by Stur (1883, 1885) on well preserved and well-characterised material of *D. karwinensis* Stur, 1883, showing prominent oval sori uniformly arranged at the apex of pinnule lobes. Pfefferkorn (1978) undertook revision of the genus *Discopteris* and of Stur's type material, providing a revised generic diagnosis, particularly with respect to the number of sporangia (12 – 100) within each sorus, and also of the vegetative material; his illustrations show the sorus developing as a depression, without an indusium, upon the lamina of the sphenopterid foliage, and they do not form a specialised structure projecting beyond the pinnule lamina. Brousmiche (1977) reviewed the generic diagnosis, which was considered subsequently (Brousmiche, 1983) in conjunction with a systematic description of *Discopteris* from the Saar-Lorraine Coalfield, in which she contested Pfefferkorn's viewpoint that the sporangia are annulate. In her description of Saar-Lorraine material, fertile material assigned to the genus *Discopteris* included three different kinds of sori: (i) with a "cupulate" structure extending beyond the pinnule lamina (*Discopteris occidentalis* Gothan, 1954), (ii) material in which sori are diffuse oval depressions on the pinnule lamina (*D. danzei* Brousmiche, 1983) and (iii) other material, assigned only with qualification, in which sori situated at the apex of pinnule lobes show a stellate structure of up to 7 ovoid sessile sporangia *("Discopteris" opulenta* Danzé, 1956). The form and disposition of the two latter types offer the closest comparison with the material at hand. Both Pfefferkorn and Brousmiche underline the association between fertile material assigned to *Discopteris* and a distinctive aspect of sphenopterid vegetative foliage; the identification of present material with this style of vegetative foliage is discussed further in the species comparisons. With respect to the stratigraphic range of material attributable to *Discopteris*, it is appropriate to note that certainly two of the specimens illustrated from the Dunkard flora in the Appalachian region, eastern North America, by Fontaine & White (1880, pl. III, Figs 2-3) as *Sphenopteris acrocarpa* sp. nov. (attributed to *Discopteris* by Wagner & Álvarez-Vázquez, 2010b) correspond closely to *Discopteris karwinensis*. If these two species should prove to be synonyms, the American taxon would have priority.

Remarks on figured specimens: The holotype (Figs 4a-b) consists of two partially superimposed fragments of pinnae of the penultimate order with lateral pinnae inserted subperpendicularly. Pinnules five-lobed to seven-lobed, showing the characteristic convex lamina. A narrow flange connects adjacent pinnules. Pinnae of the last order taper gradually towards a very small apical pinnule which is similar to a pinnule lobe. The gradual lengthening of pinnules by apical growth is visible in the paratype illustrated in Figs 5a-b, 6, with the progressive transformation into small pinnae. A more advanced stage of lengthening by apical growth is represented by the specimen of Figs 7a-b, which shows small pinnae with slightly lobate pinnular elements of approximately ovate shape modified by barely developed angular lobes. The transition from small pinnules to increasingly lobate, lengthened pinnules leading into small pinnae of the last order is very gradual. Punctate rachises of antepenultimate order are illustrated on Fig. 8a. Fertile material showing progressive appearance and maturity of sori, is illustrated on Figs 10, 11, with sporangial structures developing as

Figure 5. **a)** Paratype, x 1. Pinna of antepenultimate order. **b)** Paratype, x 6. Partial enlargement of Fig. 5a. Pinna of antepenultimate order, bearing penultimate order pinnae inserted at a wide angle. Note basal catadromous last order pinnae are essentially of similar development to next adjacent pinnae. RHW loc. 4298, La Magdalena. Donated by J.V. Casado.

Figure 6. Paratype, x 3. Partial enlargement of Fig. 5a. Pinna of antepenultimate order. RHW loc. 4298, La Magdalena.

oval depressions on the pinnule lamina near the apex of pinnule lobes. Maturity of these sporangial structures is marked by withdrawal of the pinnule lamina. The relatively coarse grain of the silty lutite on which these specimens are imprinted, does not allow the sporangial units to be photographed in detail. However, direct observation of fertile specimens suggests an agglomeration of up to eight oval sporangia sited on the remnant pinnule lamina, which has become reduced to an apparent stalk representing the pinnule midrib.

The specimen illustrated here as Fig. 8a is the same as that figured partially by Castro (2003, lám. 5, Fig. 1; lám. 6, Fig. 6; 2005, lám. 15, Fig. 1). On the other hand, our Figs 7c-d only depict part of Castro's specimen (2003, lám. 6, Figs 3-4).

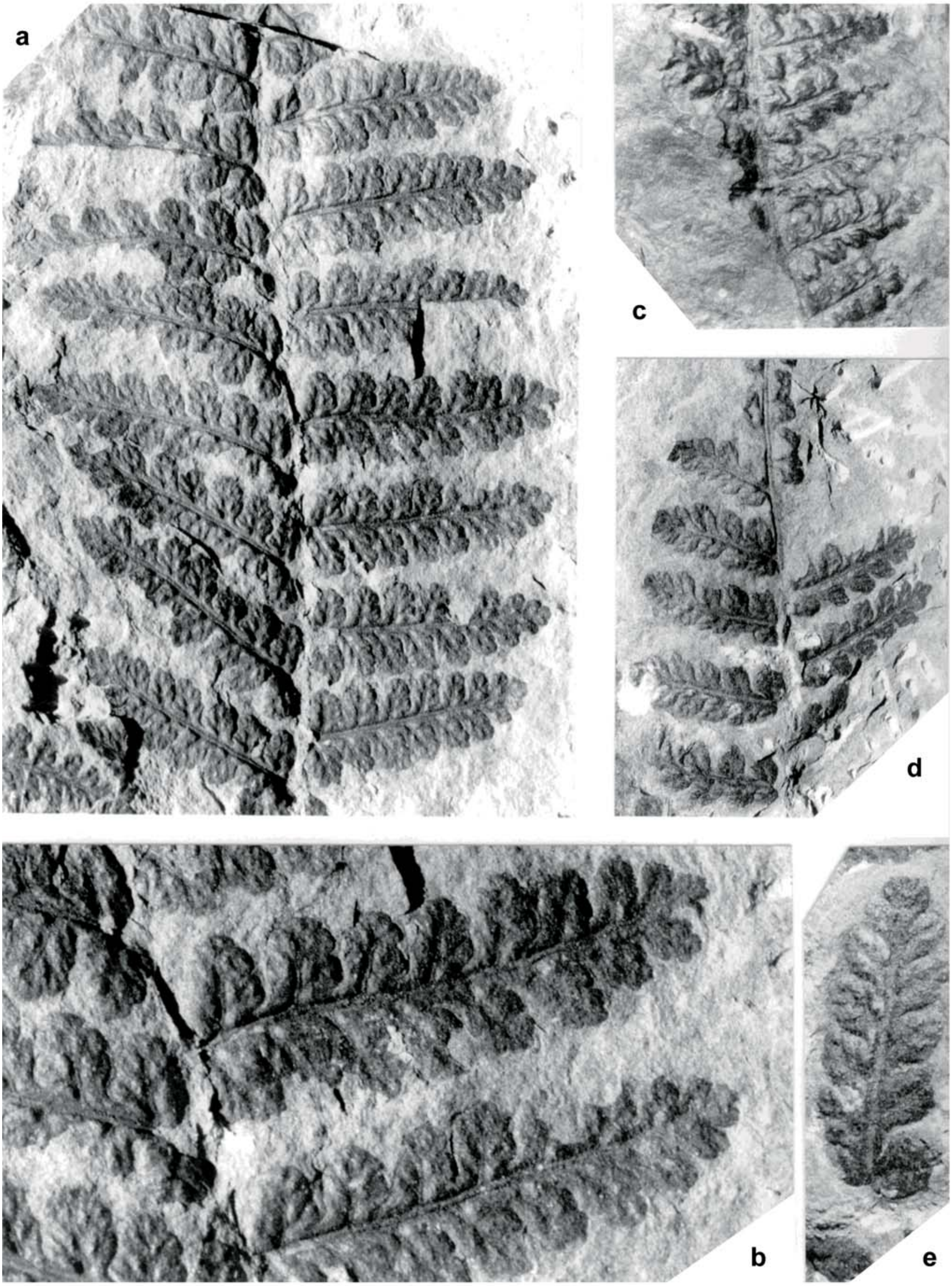
Vegetative remains of *Sphenopteris hadrophylla* from the Sabero and Ciñera-Matallana coalfields in NW Spain are depicted in Figs 13a and b, respectively. Fig. 13a shows a specimen of the unpublished protologue of *Sphenopteris hadrophylla* Knight, 1975, from the Sabero Coalfield.

Comparisons: The small fragment from the Stephanian of Saar-Lorraine figured by Brousmiche (1983, pl. 78, Figs 3, 3a) as comparable (but not identical) to *Discopteris danzei*, is considered here to be closely comparable with *Sphenopteris hadrophylla*. Unfortunately, the specimen figured by Brousmiche is rather poorly preserved. Although the size and lobing of its pinnules are comparable to the characters shown by *Sph. hadrophylla*, the outline of the lobes is too indistinct for a reliable identification. Brousmiche's specimen shows apparent sporangiate units in the distal parts of pinnae with no apparent reduction of pinnule lamina. The organisation of sporangial units is indeterminate. Although Brousmiche (1983, pl. 78 – explanation) was inclined to attribute this specimen to *Discopteris danzei*, she hesitated because of its different stratigraphic position (Stephanian, Flöz Wahlschied, attributed to the *Alethopteris zeilleri* Zone by Cleal, 2008; this corresponds to Saberian as introduced by Wagner & Álvarez-Vázquez, 2010a). *Discopteris danzei* was originally described from Westphalian C (Bolsovian) strata (*op. cit.*). Quite apart from the rather poor quality of the Stephanian specimen figured by Brousmiche (1983, pl. 78, Figs 3, 3a), its tentative identification with *Discopteris danzei* may be questioned because this species apparently possesses more individualised pinnules with a more triangular outline.

Sphenopteris weissii (Potonié, 1893) Němejc, 1936 is also comparable. The authors have benefited from a set of photographs of the counterpart specimen of the holotype of *Sphenopteris weissii* which has been kindly made available by Dr. S. Schultka of the Museum für Naturkunde, Berlin (*pers. comm.*, 26.03.1999). The illustration of the type specimen, (Potonié, 1893), and photographs of the counterpart show that the general aspect and size of pinnules of this species are similar to, but generally smaller than those of *Sphenopteris hadrophylla*. Moreover, *Sph. weissii* shows slightly more elongate pinnules in pinnae of equivalent development, as well as a tendency to possess more pointed lobes than occur in the somewhat squatter pinnules with more rounded lobes of *Sph. hadrophylla*. Pinnules in *Sph. hadrophylla* have a correspondingly more blunt and squarish appearance. The highly characteristic vaulted nature of the pinnules of *Sph. hadrophylla*, which is indicative of a thick pinnule lamina, is not displayed to the same extent in *Sph. weissii*, although preservation possibly plays a role. Even so, the pinnules of *Sph. weissii* are not devoid of relief. It is further noted that Potonié (1893, Taf. IV, Fig. 1c) illustrated a clearly aphleboid basal catadromous pinna of the penultimate order, in which the dissected nature of the pinnules and their lobes is apparent as well as the acute apices. In contrast, the basal catadromous pinnae of *Sphenopteris hadrophylla* are not developed differently to the adjacent lateral pinnules and where there is an apparent more extensive development (Fig. 8a), there is no loss of lamina as in *Sph. weissii*. The style of pinnule development in *Sph. weissii* seems to have been of a rather gradual apical type similar to that of *Sph. hadrophylla*, but the few specimens figured are insufficient to permit a full comparison of each different developmental stage. In *Sph. weissii* the pinnule bases tend to be constricted at the stage of the development of the second lobe, at which stage pinnule bases in *Sph. hadrophylla* are still confluent, albeit weakly constricted and decurrent. Subsequently, pinnules become more separated and appear more distant very early on in the pinnule development of *Sph. weissii* and its pinnae appear somewhat more delicate and more incised. Last order pinnae are more slender and acutely tapering, and the terminal in *Sph. weissii* is small, relatively well-individualised and slender. Pinnae do not have the more parallel-sided appearance and blunt terminal of *Sph. hadrophylla*.

Wagner (1964) mentioned *Sphenopteris weissii* in a list of plant fossils from the La Magdalena coalfield (province León) in NW Spain. The corresponding pinna fragment was illustrated by Álvarez Ramis (1965, lám. XXI, Figs 3, 3a), to whom this specimen was made available by one of the present writers (RHW) with the annotation *Sphenopteris* aff. *weissii*, a provisional identification maintained in publication (Álvarez Ramis, 1965, p. 39). It is noted that although she referred to this specimen as belonging to the Jongmans Collection, it was collected from locality 331 of Wagner, near the village of Garaño at La Magdalena. Álvarez Ramis (1965, pl. XXI, Fig. 2) also figured a specimen from the Villablino Coalfield in NW Spain as *Sph.* aff. *weissii*. Both remains appear attributable to *Sphenopteris hadrophylla*.

The somewhat similar species *Sphenopteris wagneri* Álvarez Ramis, 1965 possesses larger, more elongate pinnules, as well as aphleboid pinnules at the base of


a
c
d
b
e

pinnae. This species was attributed to *Discopteris* by Castro (2005), who has produced the best illustrations. *Sph. hadrophylla* differs by possessing squatter, less elongate, lobing pinnules characterised by more rounded lobes. *Sph. hadrophylla* also lacks the deeply dissected aphleboid pinnules with almost linear segments which characterise both *Sph. wagneri* and *Sph. weissii*.

Professor M. Barthel and Dr S. Schultka (*pers. comm.*) have drawn the writers' attention to another species of *Sphenopteris* with relatively small, vaulted pinnules, viz. *Sphenopteris deichmuelleri* Sterzel, 1893. This species, originally described on the basis of a single, very fragmentary, terminal part of a pinna of apparently penultimate order (Sterzel, 1893), has been illustrated and described more adequately by Barthel (1958, p. 47, Taf. XI, Figs 1-3, Taf. XII, Figs 1-4). This included a photographic illustration of the type which was figured originally by means of drawings. *Sph. deichmuelleri* shows more triangular pinnules with acute pinnule lobes and a clearly developed, narrow flange extending downwards along the rachis from the obliquely inserted pinnules. *Sph. deichmuelleri* is more similar to *Sph. weissii* and *Discopteris wagneri* than it is to *Sph. hadrophylla* which possesses squatter, more nearly perpendicular inserted pinnules with rounded, angular lobes which are not pointed. On the whole, the pinnae of *Sph. hadrophylla* appear more compact than the more gracile ones of *Sph. deichmuelleri*, which Barthel (2006) has most recently attributed to *Sph. mathetii* Zeiller *in* Renault & Zeiller, 1888. (It is immaterial to the present paper to discuss whether this latter attribution is correct or not.)

Comparison might also be made with *Sphenopteris rossica* Zalessky, 1937, another Stephanian species with very small pinnules. However, in this case the pinnae are much less compact, with very small pinnules ranging from trilobate to quintulobate, and showing a thinner pinnule lamina. This very graceful fern is quite different from the more robust *Sph. hadrophylla*.

Professor Barthel and Dr. Schultka (*pers. comm.*) also drew the writers' attention to *Sphenopteris dechenii* Weiss, 1869, another Rotliegend species with small pinnules. A photograph of the type was made available by Dr. Schultka and shows a more thin-limbed species with more or less ovoid pinnules which are connected by a narrow flange along the rachis and which are entire to slightly lobate. Weiss (1869-72, Taf. VIII, Figs 2, 2a-b) illustrated his species by drawings which have obviously confused subsequent workers, such as Zeiller (1892, pl. I, Figs 1, 1A-B), who figured a specimen of *Senftenbergia elaverica* (Zeiller, 1888) Wagner, 1999 as *Sphenopteris dechenii*. The specimens figured as *Sph. dechenii* by Álvarez Ramis (1965, p. 50-51, lám. XXXII, Figs 1-3; lám. XXXIII, Figs 1-3), from Villablino (León, NW Spain), represent pinna fragments with non-lobate, ovoid pinnules which are different to those of *Sphenopteris dechenii*. These specimens are most likely attributable to *Pseudomariopteris cordato-ovata* (Weiss, 1869) Gillespie, Clendening & Pfefferkorn, 1978.

The diagrammatic nature of the illustrations of the type specimens (Fontaine & White, 1880) makes for difficult comparison with *Sphenopteris minutisecta* Fontaine & White, 1880, a species described on material from the basal Dunkard measures in the central Appalachian region of North America. This species has been regarded most recently as a synonym of *Renaultia lebachensis* (Weiss, 1869) Brousmiche 1983, a more thin-limbed fern (Wagner & Álvarez-Vázquez, 2010 b). It has been variously interpreted by different authors.

Another, somewhat comparable species is *Sphenopteris pseudo-marrati* Danzé, 1956, which is also characterised by a thick pinnule lamina and apical pinnule development. However, its pinnules are broader and more rounded, with lobes that are also very rounded and semicircular (Danzé, 1956). Last order pinnae are narrowly triangular and more obviously tapering and the slender terminal is small and clearly fused, with very rounded lobes.

Sphenopteris rutaefolia Gutbier, 1835 is even less comparable, with apical development with a critical number of 4. Although it possesses a relatively thick pinnule lamina, its lobes appear to be flatter and are more rounded and less inclined. Pinnules are at every stage more elongate than in *Sphenopteris hadrophylla*, and, on attaining the pinna stage have a length/breadth ratio of about 3:1. Longer pinnules give the pinnae a wider, more spreading appearance; they are also more tapering and broadly triangular. Pinna terminals are more slender and acuminate, being also more individualised. Rachises are also more slender and characteristically show a flexuous ridge on their surface. The pinnule lamina of *Sph. rutaefolia*, although rather thick, is not quite as coriaceous as in *Sph. hadrophylla*, and the venation is not so strongly marked and deeply imbedded.

Sphenopteris douvillei Zeiller, 1888 from the Westphalian of northern France (Zeiller, 1886-88; Danzé, 1956) is distinguished by its more deeply incised, markedly inclined and sharply pointed lobes. Pinnules attain the pinna stage soon after the third pair of lobes have been

Figure 7. **a)** Paratype, x 3. Pinna of penultimate order with subperpendicular pinnae showing tri- to quintulobate pinnules. **b)** Paratype, x 6. Partial enlargement of Fig. 7a. **c, d)** Paratype, x 6. Fragments of pinnae of the penultimate order showing small pinnules. **e)** Paratype, x 3. Enlargement of the second pinna of the left hand side of Fig. 7d. RHW loc. 4298, La Magdalena.

Figure 8. **a)** Paratype, x 3. Pinnae of penultimate order alternately arranged on a punctate rachis of penultimate order, itself inserted perpendicularly on a punctate rachis of antepenultimate order. **b)** Paratype, x 3. Near-terminal fragment of penultimate order. RHW loc. 4298, La Magdalena.

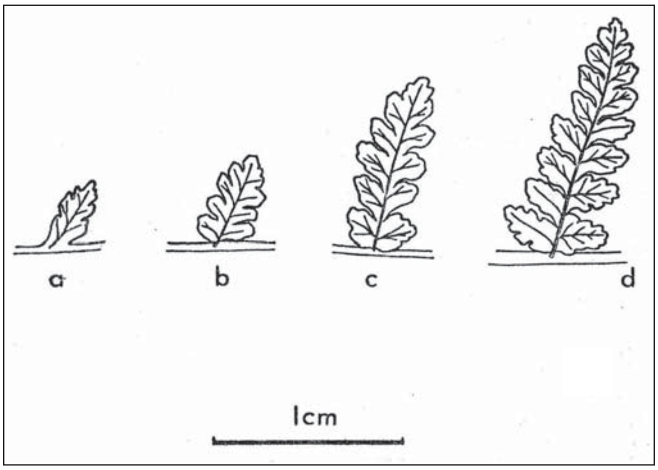


Figure 9. Illustration of pinnule development. **a)** Rather elongate pinnule from near the terminal of a last order pinna. RHW loc. 1099, Ciñera-Matallana. **b)** Pinnule attaining the common stage of four pair of lobes. Knight loc. 133a, Sabero. **c)** Elongate pinnule shape as the pinna stage is attained with five pairs of lobes. Knight loc. 133a, Sabero. **d)** Pinna with basal pinnules attaining three pairs of lobes. Knight loc. 63, Sabero.

developed (critical number of 3). At this stage the basal lobes are already incised with clear secondary lobes; consequently its pinnae have more dissected aspect than those of *Sphenopteris hadrophylla*.

The thick coriaceous pinnule lamina prompts comparison with *Discopteris occidentalis*, and, in particular, the material figured by Danzé (1956) as *D. bertrandii* Danzé, 1955b which has been placed in synonymy with *D. occidentalis* by Brousmiche (1977). Danzé's material is characterised by triangular pinnules with very rounded lobes, and a critical number of 7, the pinnules being much more elongate. The basal basiscopic lobe of a pinna becomes expanded into a "pseudo-aphlebia", a characteristic not seen in *Sphenopteris hadrophylla*. Venation is less regular than in the latter, the lateral veins being curved, irregularly forked and bunched.

Remarks on synonymy: *Sphenopteris hadrophylla* is an easily recognisable species on account of its robust appearance and coriaceous surface. Although rare, it has been encountered in a number of the post-Asturian coalfields (upper Barruelian, Saberian and Stephanian B) in the province of León, NW Spain. It has also been identified, albeit tentatively, from the Narragansett Basin in eastern North America (Wagner & Lyons, 1997, p. 279; originally figured as *Sphenopteris minutisecta* by Lyons & Darrah, 1978). It is comparable but not identical to a number of species from northern Europe, as detailed in the previous chapter.

The only figures in the literature on the Stephanian floras of NW Spain that can be referred to unhesitatingly as *Sphenopteris hadrophylla* are two fragments published by Álvarez Ramis (1965, 1967) as *Sphenopteris* aff. *weissii* Potonié. One of these remains, originating from the Saberian of La Magdalena (León), had been listed previously by Wagner (1964) as *Sphenopteris weissii*. This specimen, although small, is undoubtedly identifiable as the present species, and represents the terminal part of a pinna of the penultimate order. The second specimen figured by Álvarez Ramis (1965) as *Sphenopteris* aff. *weissii* is from the Villablino Coalfield (León), from the "Paquete Lumajo" (probably the Antracitas beds belonging to lower Stephanian B) near the village of Villaseca. It is a very small fragment of the near-terminal part of a penultimate order pinna, which appears to correspond unmistakably to *Sphenopteris hadrophylla*. The single fragment figured and described by Álvarez Ramis (1965, 1967) from the Leitariegos mountain pass (Antracitas beds, lower Stephanian B) in the Villablino Coalfield, under the name of *Sphenopteris lebachensis* Weiss, 1869, is clearly attributed incorrectly and might well belong to *Sphenopteris hadrophylla*. However, it is poorly illustrated, so the comparison can only be tentative.

Localities in the Cantabrian Mountains, NW Spain: With the exception of the Sabero Coalfield, all collecting locality numbers refer to the locality sequence commenced by R.H. Wagner and continued in collections of the Palaeobotanical Section of the Real Jardín Botánico de Córdoba. Lithostratigraphic units are as stated alongside columns of Fig. 3. No unified stratigraphic column exists for El Bierzo (see Fig. 2 for its geographic position).

La Magdalena (León) (Saberian):

331 – Near Garaño, in the northern part of the coalfield (Wagner, 1964; Álvarez Ramis, 1965, 1967 – as *Sphenopteris* aff. *weissii*). Interval 1 of Wagner & Castro (2011).

4298 – La Luisa opencast mine east of Garaño in the lower part of the succession. Interval 1.

9612 – North of Garaño. Section on the road La Magdalena to Barrios de Luna. South of the marker km 2. Interval 2 of Wagner & Castro (2011).

9617 – North of Garaño, in anticlinal core, several closely spaced, thin plant-bearing horizons, lower part of the La Magdalena succession Interval 2, without further precision.

Ciñera-Matallana (León) (Saberian):

355 – Spoil heap of an abandoned coal mine at c. 550 m East of the Cueto de San Mateo mountain top. San José Formation?

1099 – Roadside locality at 600 m SE of Pola de Gordón, San José Formation.

1431 – Valcayo section, Matallana Syncline, at 210.20 m above the base of the Bienvenidas Formation.

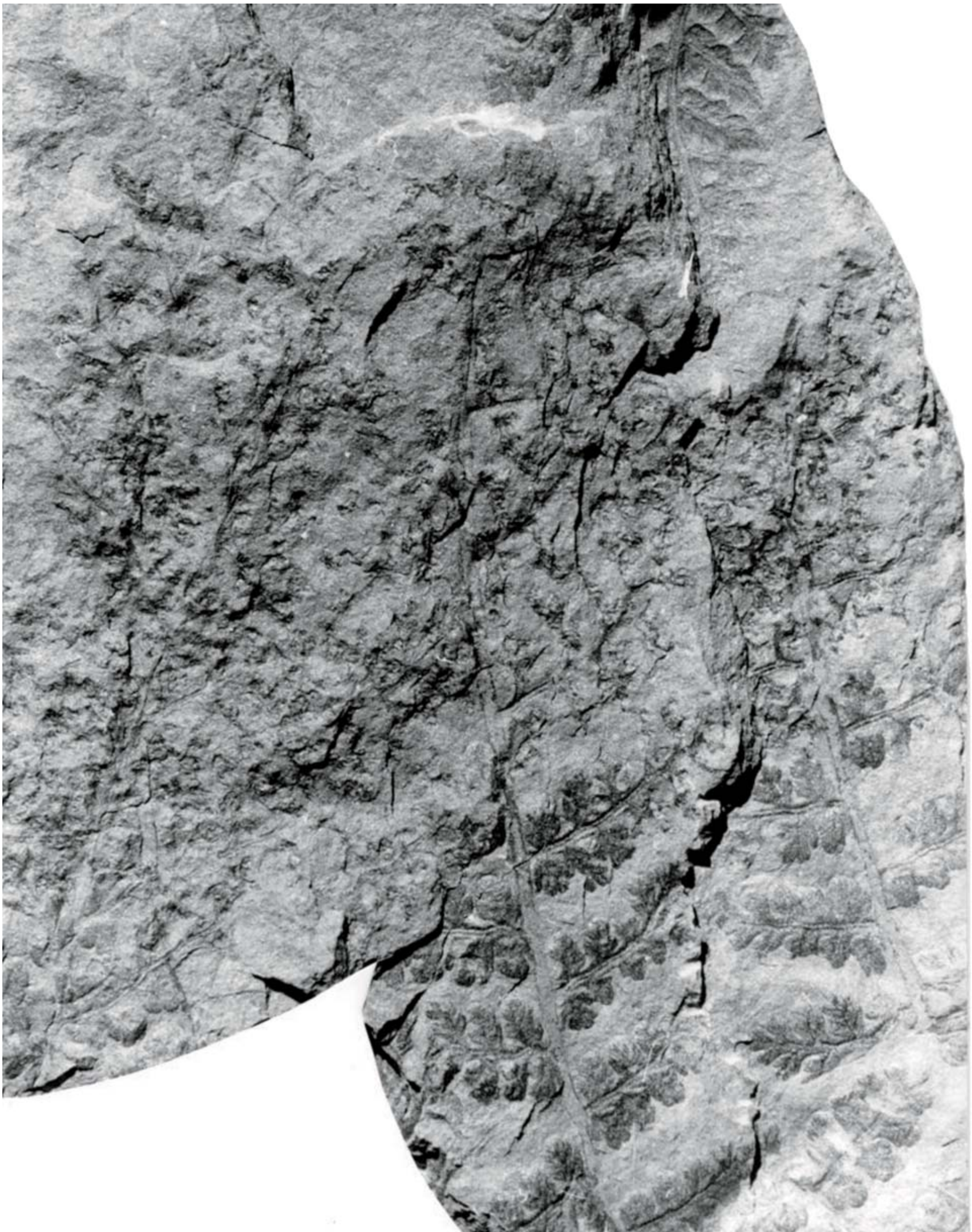


Figure 10. Paratype, x 3. Frond fragment showing three consecutive pinnae of the penultimate order with distal parts in fertile condition. Development of sori occurs on the lamina of distal pinnule lobes of partially fertile pinnae. The more advanced development of sori on higher pinnae is marked by withdrawal of the pinnule lamina and ultimately reduction of the midrib to a stalk bearing a sporangial agglomeration of synangial aspect. RHW loc. 4298, La Magdalena.

Figure 11. Paratype, x 6. Partial enlargement of Fig. 10 to show more clearly the fertile areas in the distal parts of pinnae, with withdrawal of the pinnule lamina around developing sporangial agglomerations. RHW loc. 4298, La Magdalena.

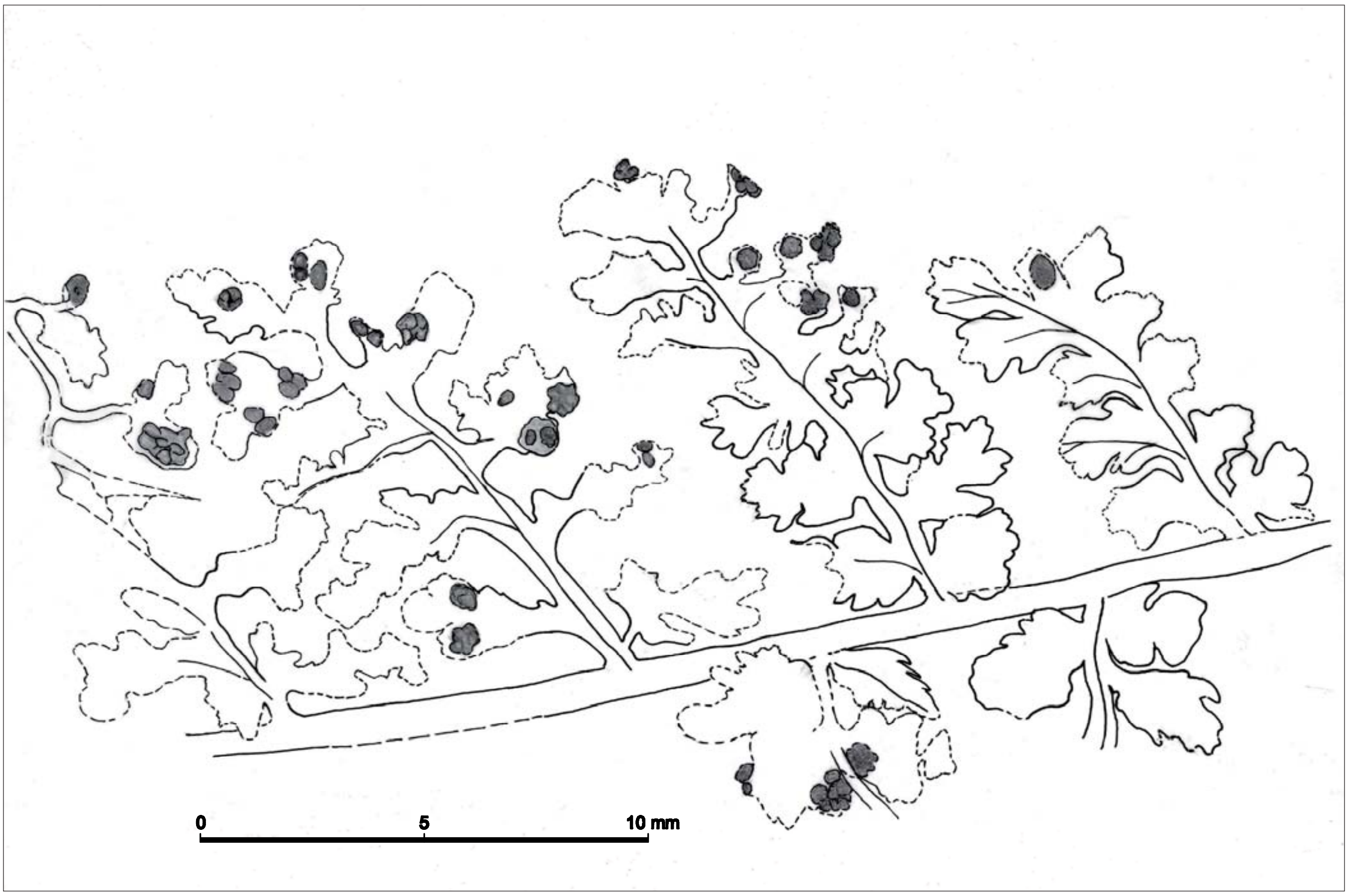


Figure 12. Interpretation of the emplacement and development of sori on the partially fertile pinnae illustrated on Figs 10 and 11. Tracing prepared from an enlargement of the rachis and pinnae illustrated on the left half of Fig. 11.

1855 – Llanagallegos, Roguera Formation, roof shales of non-workable coal at 25 m below seam 5 of San José (with cf.).

1964 – 450 m East of Tabliza Valley, northern flank of Llombera Syncline, roof shales of seam 4 of San José Formation.

2248 – Amézola coal mine, 2nd level, 1st gallery below coal seam Amézola 8 (?), at 53 m West, Pastora Formation.

2448 – Outcrop in the path to Collalampa at 1370 m NW of intersection between the road to Llombera and the main street of Llombera (with cf.). San José Formation.

4255 – Tabliza area, borehole 43, at 322 m depth, 80 m above seam 5 of San José Formation (with cf.).

Villablino (León) (Stephanian B):

Leitariegos, Antracitas beds, Jongmans Collection (Álvarez Ramis, 1965, 1967 – figured as *Sphenopteris lebachensis* Weiss).

Paquete Lumajo (Antracitas beds), near Villaseca (Álvarez Ramis, 1965, 1967 – as *Sphenopteris* aff. *weissii*).

5185 – Antracitas cross-cut, roof of seam 19bis, Antracitas beds in lower part of the succession.

El Bierzo (León) (Saberian or Stephanian B) (for localities see Fernández-García *et al.*, 1984):

3621 – Bembibre/Torre del Bierzo area, Campomanes mine.

3338 – Alto Bierzo, Lomba section, about 1 km SE of Matarrosa, East of río Sil, 108.75 m from base of section.

9376 – Toreno-Valdesamario area, Bierzo Oriental. Arroyo de San Esteban section, at 69.50 m from base of section.

Sabero (León) (Saberian):

(Collecting locality numbers refer to the number sequence of J.A. Knight; see Knight 1983a).

63 – Mine cross-cut 4E-3S, 4th level of Pozo Sotillos, roof of Capa 1, Herrera Beds.

110 – Roadside tip between Olleros and Sotillos, from workings of the abandoned mine “3er piso de Olleros”, working primarily the Herrera Beds and Unica Beds.

113 – Small tip in valley W of Casetas, from seams probably attributable to the Herrera Beds.

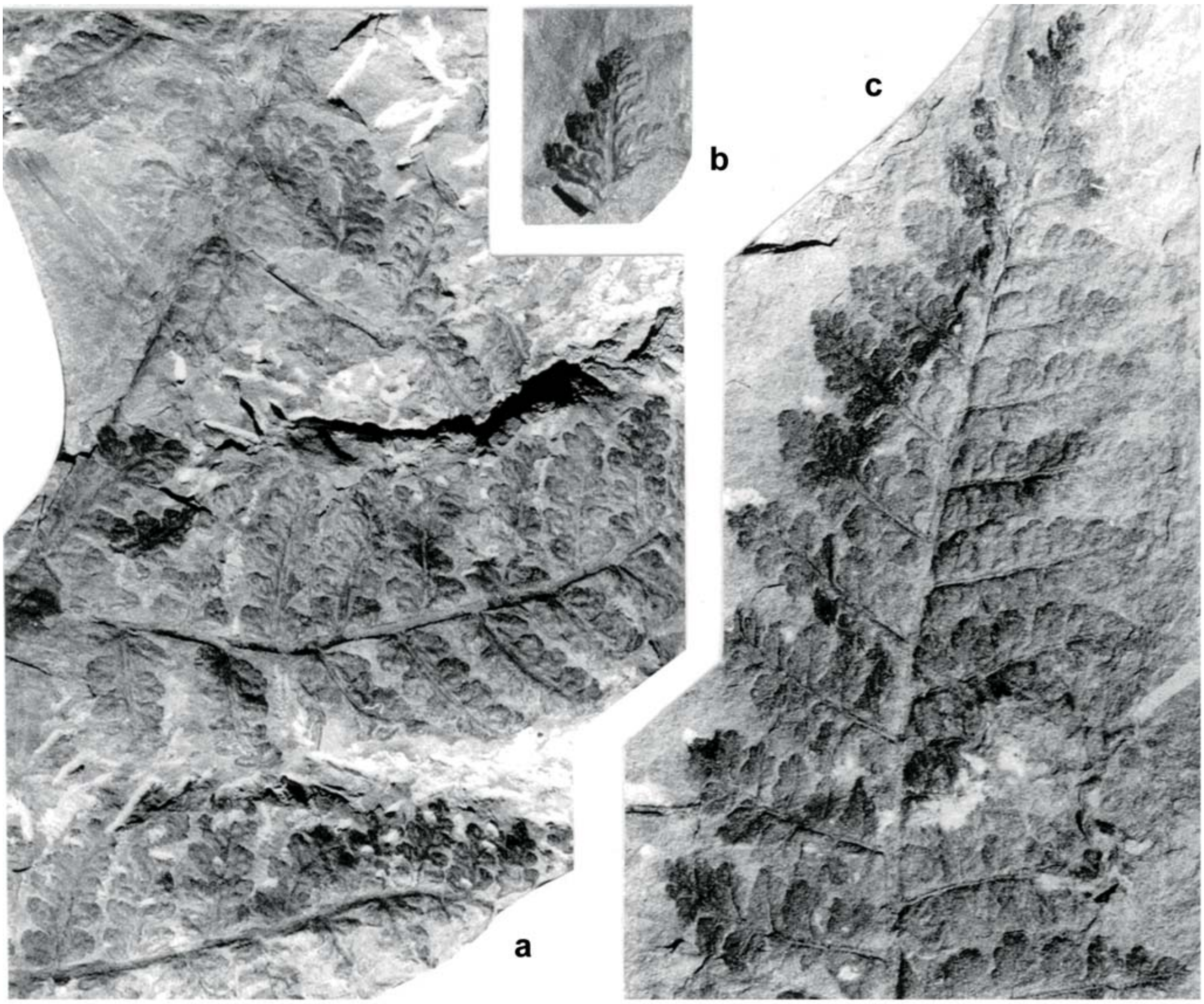


Figure 13. a) Specimen (x 3) illustrated as unpublished protologue of *Sphenopteris hadrophylla* Knight, 1975. Knight loc. 133a, Unica Beds, Sabero. **b)** Specimen (x 3) from Ciñera-Matallana Coalfield. RHW loc. 1964, roof of seam 4ª de San José, San José Formation. **c)** Paratype, x 3. Pinna terminal on underside of same slab as fertile material illustrated on Figs 10 and 11. RHW loc. 4298, La Magdalena

113a – Measured section 9, SW of Sotillos, Unica Beds.

149 – Measured section 12, near the disused Pozo El Peñón, from the small tip on the Capa Ancha, Unica Beds.

ACKNOWLEDGEMENTS

Professor M. Barthel and Dr. S. Schultka are thanked for helpful suggestions and the provision of photographs of the types of *Sphenopteris weissii* (Potonié) and *Sph. dechenii* Weiss, both in the collections of the Museum für Naturkunde, Berlin. Excursions with Dr. M.P. Castro in the La Magdalena Coalfield have helped to augment the already substantial collections from this area. J.V. Casado kindly donated the splendid specimen from La Magdalena figured here as Figs 5, 6. Fruitful discussions with Dr. C. Álvarez-Vázquez are gratefully acknowledged, as is her technical assistance. The referees, Drs C.J. Cleal and J.B. Diez, are thanked for thorough reviews which allowed improvements in the text.

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Manuscrito recibido: 23 de febrero, 2012
Manuscrito aceptado: 13 de abril, 2012