



The *Struthiopteris spicant* (Blechnaceae, Polypodiopsida) complex in Western Europe, with proposals for taxonomic and nomenclatural changes

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Abstract

Struthiopteris spicant is a medium-sized, dimorphic fern that occurs mainly in Western Europe and Western North America. The species is quite variable, with several forms differing in frond sizes and degree of dimorphism. In addition to the typical plant, in Europe two other varieties are recognized: the Iberian *S. s.* var. *homophyllum* includes plants up to 20 cm, monomorphic or subdimorphic, with fragmented cenosori; the Icelandic *S. s.* var. *fallax* comprises very small plants up to 5 cm, monomorphic, with isolated sori. Outstanding questions remain about hybridization among the different forms, their taxonomic status, and the relations between different populations. The present work aims to study additional morphological and anatomical features of the *S. spicant* complex in Western Europe using a statistical approach, to resolve the taxonomic position of the different forms. We observed traits ranging from the rhizome scales to the spores and used one-way ANOVA to test for significant differences between all varieties and PCA to determine whether plants assigned to different varieties can be classified statistically into distinct groups. We detected significant differences in several of the analysed traits among the varieties in the complex. Qualitative differences in pinna anatomy and epidermal cells also help segregation of the varieties considered. Our results allowed us to propose a new specific status for the Icelandic endemic var. *fallax* and a new endemic Spanish variety, *S. s.* var. *pradae*.

Keywords Endemism · Morphology · Pteridophytes · Taxonomy

Handling Editor: Ricarda Riina.

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Introduction

Blechnaceae Newman is a subcosmopolitan family of leptosporangiate ferns (Polypodiopsida) that includes around 250 species (PPG1 2016). Until recently, most of this diversity fell into one large genus, *Blechnum* L., but after evidence accumulated concerning its non-monophyletic status (Shepherd et al. 2007; Gabriel y Galán et al. 2013; Perrie et al. 2014; Gasper et al. 2017), *Blechnum* was split into several entities (Gasper et al. 2016). In its current conception, Blechnaceae as a whole is made up of 24 genera (PPG1 2016).

The genus *Struthiopteris* Scop., as currently defined, was resurrected by Gasper et al. (2016) to accommodate small to medium size, dimorphic, pinnate species (Fig. 1). It contains five species, with a northern geographical distribution. Four of these species are restricted to eastern Asia, in Japan and Taiwan: *Struthiopteris niponica* (Kunze) Nakai, *S. hancockii* (Hance) Tagawa, *S. amabilis* (Makino) Ching, and *S. castanea* (Makino) Nakai (Iwatsuki 1992; Chiou et al. 1994).

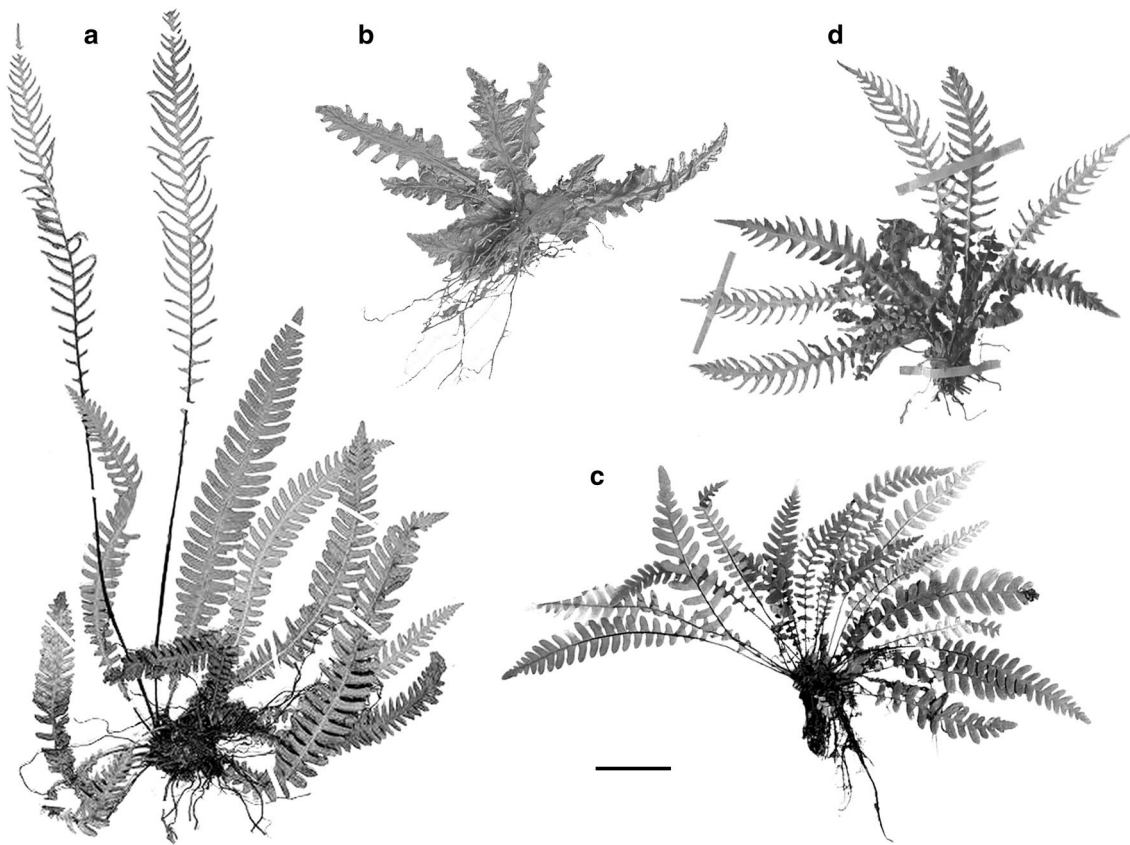


Fig. 1 Forms of plants within the *Struthiopteris spicant* complex. **a** Dimorphic: *S. spicant* var. *spicant* (MA 747921); **b** monomorphic: *S. spicant* var. *fallax* (MACB 109359); **c** monomorphic: *S. spicant*

var. *homophyllum* (MACB 1092626); **d** subdimorphic: *S. spicant* var. *homophyllum* (MACB 32367). Bar=2 cm in **a**; 1 cm in **b**; 2.5 cm in **c, d**

The fifth species, *S. spicant* (L.) Weiss, is the object of the present study. This taxon is described as a terrestrial or saxicolous plant, living on acid or neutral soils, with dimorphic fronds: the sterile ones are lanceolate, pinnatisect, and forming a basal rosette of 20–70 cm long, and the fertile ones are erect and longer, with heavily contracted pinnae which bear costal cenosori and have continuous indusia (Rolleri and Prada 2006). This species occupies a larger distribution than its congeners, occurring in almost all of Europe (from Sweden, Poland, Ukraine, and Romania westwards to Iceland and the Iberian Peninsula), some parts of Northern Africa (where it is rare), the Macaronesian archipelagos (Canary Islands, Madeira, and Azores Islands) and the Pacific Northwest area of North America (USA: California, Oregon, Washington, Alaska; Canada: British Columbia). It is typically a very common element in a variety of habitats, particularly in forests (Lawalrée 1964; Nauman 1993).

Such a wide range has allowed a certain amount of morphological variation to emerge, which is mainly manifested as differences in frond sizes and degree of dimorphism. Thus, plants can be: a) dimorphic, in which there are two highly different types of fronds associated with function: the

sterile fronds have expanded pinnae without sporangia while the fertile ones are much longer and have highly contracted pinnae without green tissue at maturity (Fig. 1a); b) monomorphic, in which all fronds are similar in morphology, irrespective of the presence of sporangia (Fig. 1b, c); or c) subdimorphic, in which some fronds, regardless of whether they bear sporangia or not, are equal or slightly longer than the rest, with slightly contracted pinnae (i.e. when fully developed, they are, at least partially, narrower but with a clear area of green tissue) (Fig. 1d).

This variation in frond morphology in *Struthiopteris spicant* has been the subject of previous research (e.g. Löve and Löve 1966). Taxonomists have described several entities that have been formally recognized with different taxonomic assignments, usually as subspecies or, more frequently, as varieties or ecological forms. In consequence, *S. spicant* can be seen as a morphological complex. While most of its forms have ultimately been considered to fall under the expected variation of *S. spicant* s.l. and thus have been neglected in local floras, some of them are widely accepted and regularly included in floras and taxonomic treatments. For example, the Pacific American plants fit the general

dimorphic morphology of *S. spicant* but with larger sterile fronds, up to 100 cm (Löve and Löve 1968). Variety *homophyllum* (Merino) Gabriel y Galán & R. Pino (Wasowicz et al. 2017b) comprises smaller plants, with erect fronds up to 20 cm, usually all sporogenous, monomorphic or subdimorphic, and with the cenosori typically fragmented and the indusia discontinuous (Merino 1898; Ormonde 1986). This variety is endemic to the northwest of the Iberian Peninsula, in both Spain and Portugal (Ormonde 1986; Molino et al. 2018). Finally, var. *fallax* (Lange) Wasowicz & Gabriel y Galán comprises very small plants, only about 2–5 cm, usually with monomorphic fronds, uncontracted pinnae, and isolated sori. It grows exclusively in Iceland, where its scarce populations live in close proximity to (and presumably are dependent on) hot springs (Wasowicz et al. 2017b).

The consideration of these distinct forms as varieties dates back to pteridologists Lange (1880) and Christ (1904). More recently, Löve and Löve (1968) observed that: a) cultured plants of *homophyllum* and *fallax* maintain their traits over time, and var. *homophyllum* is more variable than var. *fallax*; b) both have the same chromosome number, $2n = 68$, which was later corroborated by Horjales et al. (1990) for var. *homophyllum*; and c) both are completely interfertile with the typical form of *S. spicant*, so it is possible that hybrids may form if they come into contact. Based on these ideas, Löve and Löve proposed a taxonomy in which *S. spicant* (sub. *Blechnum spicant*) was divided into two subspecies: a) subsp. *nipponicum* (Kunze) Löve & Löve which includes the Pacific populations from both Japan and America (a concept which has been usually disregarded by subsequent pteridologists (e.g. Nakato 1987); and b) subsp. *spicant*, the European race, with two varieties in addition to the typical var. *fallax* Lange and var. *homophyllum* Merino. These authors never demonstrated conclusively the existence of hybrids, but did state (*op. cit.*, p. 670) about var. *homophyllum* that “at least one of the specimens we cultivated could perhaps be interpreted as a hybrid”, and about var. *fallax* that “hybrids have not been observed for the simple reason that the two populations never meet (...) but there is no reason to believe that such hybridization would not be possible if an opportunity arises”. In view of the above, *S. spicant* can be described as a complex of forms not fully understood to date. Outstanding questions remain about hybridization among the different forms, their taxonomic status, their geographical distributions, and the relations of the European and American populations to one another and to the Asian species.

In the context of a broader study focused on the whole genus *Struthiopteris*, we have undertaken a new approach to the *S. spicant* complex in Europe by applying DNA sequencing and observing new morphological features not considered by previous researchers. Regarding DNA characters, a noticeable and striking result is the very limited

genetic variation in chloroplast, nuclear, and microsatellite data between European plants from many populations and between these and American populations (unpublished data). This observation coincides partially with previous research that also included different populations of *S. spicant* (Soltis and Soltis 1988; Korpelainen and Pietiläinen 2008). The scarcity of molecular differences prevents construction of a well supported and highly resolved phylogeny that could help to elucidate the taxonomy. Here, we focus primarily on the European taxa because the variation within the North American group is still poorly known and the latter would need its own study using a comprehensive sampling. The present work aims to study additional morphological and anatomical features of plants within the *S. spicant* complex from Western Europe, in order to resolve the taxonomic position of the different forms.

Materials and methods

A total of 50 individuals from all the varieties of the complex were studied (Appendix 1). Plants came either from herbaria or from new collections (Fig. 2). At least one voucher per sampled population has been deposited in the MACB herbarium (Madrid, Biology UCM). Samples were taken to represent variation in the complex throughout the Atlantic region of Europe, including the latitudinal extremes of its distributional range: Iceland and the Canary Islands. More in-depth sampling was completed in the northeast of the Iberian Peninsula where a higher incidence of morphological variation has been detected (personal observation of the authors). A few individuals from southern France in the Mediterranean and the Alps in Austria were also included.

The following traits were observed for all specimens: size of rhizome scales (at least 3 per individual), length of sterile and fertile leaves, differentiating between petiole and laminae (at least 2 sterile and 1 fertile per individual, if possible), width at midpoint of sterile and fertile pinnae (at least 1 per frond) and anatomical characters of fertile and sterile pinna sections (2 per taxon), and the epidermis, including both adaxial and abaxial surfaces (at least two samples per taxon). In addition, we measured the width and length of 20–30 spores in at least two individuals per taxon. Figure 3 shows schematically the traits observed.

To characterize the level of sterile–fertile leaf dimorphism, we also calculated two ratios: one is the result of dividing the length of the fertile lamina by the length of its petiole (since dimorphic plants tend to elongate the fertile petiole), and the other is the result of dividing the width of the fertile pinna by the width of the sterile pinna (since dimorphic plants tend to reduce the width of the fertile pinnae).

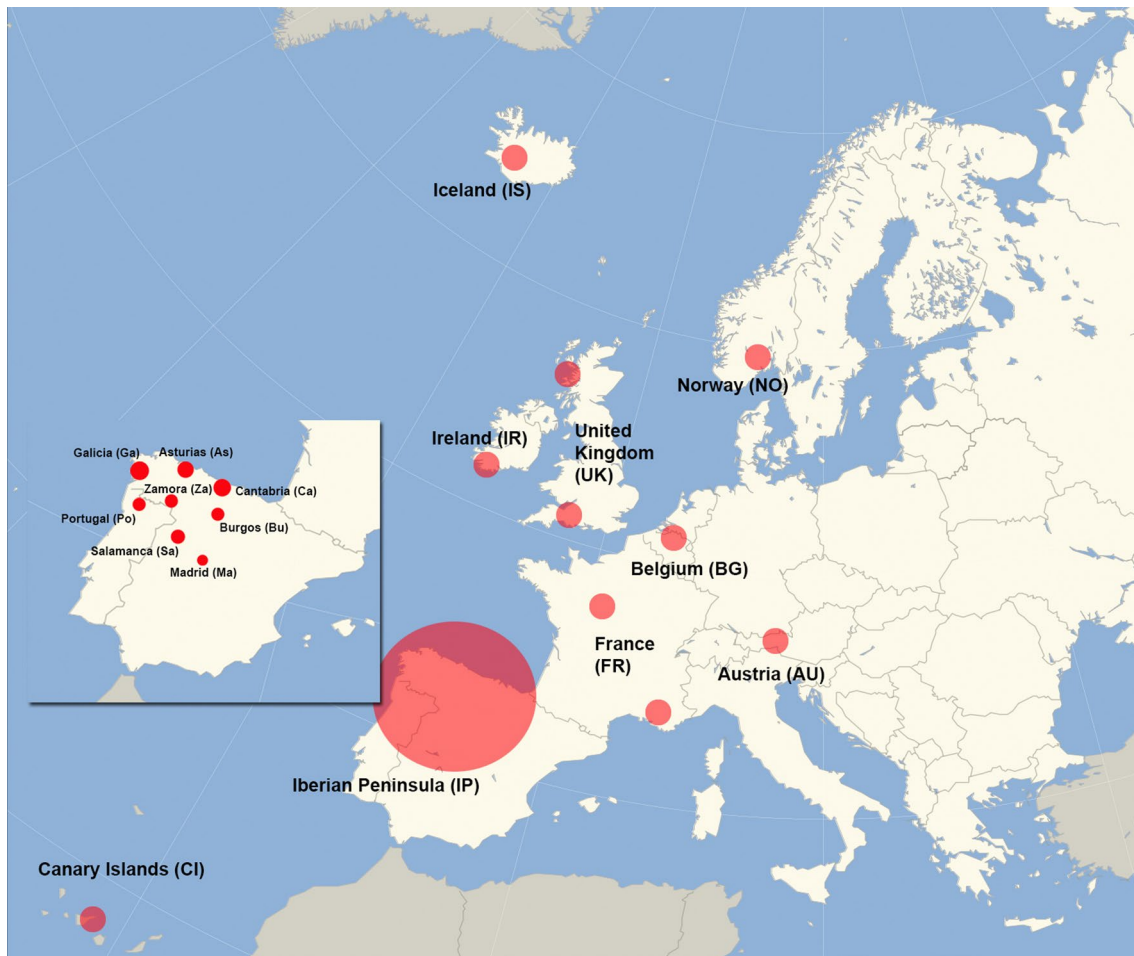


Fig. 2 Atlantic region of Europe, showing the sampling locations. This sampling covers the latitudinal extremes of the distribution area of *Struthiopteris spicant*, from Iceland in the north to the Canary

Islands (Spain) in the south. The inset map indicates with more detail the sampling locations in the Iberian Peninsula (Spain and Portugal) where a higher degree of morphological variation has been detected

The following traits were measured using a light microscope with Nikon Coolpix camera attached: 1) length of the sterile laminae, 2) width of the sterile laminae, 3) length of the sterile petiole, 4) width of the sterile pinnae, 5) length of the fertile laminae, 6) width of the fertile laminae, 7) length of the fertile petiole, 9) width of the fertile pinnae, 11) length of the rhizome scale, 12) width of the rhizome scale, 13) length of the spore, and 14) width of the spore. Key ratios between some of these variables were subsequently calculated: 8) ratio of fertile laminae length/fertile petiole length, and 10) ratio of sterile pinnae width/fertile pinnae width.

When several measurements of a particular trait were obtained from the same individual, mean values and standard deviations are reported.

Statistical analyses

We calculated basic statistics (i.e. means and standard deviations) for all measured traits and used one-way ANOVA and

post hoc Tukey test to test for significant differences between investigated morphological forms in the *S. spicant* complex. Principal components analysis was performed on the matrix containing the data from measurements of the fronds and rhizome scales in order to explore the morphospace. Significance level was set to $\alpha=0.05$ for all the tests. All statistical analyses were done with the software IBM SPSS Statistics 25 (IBM).

Results

Morphoanatomical features

The measured traits fall broadly into three classes of characters related to lamina, rhizome, and spore morphology. We detected significant differences in several of these traits among the four varieties of the *Struthiopteris spicant*

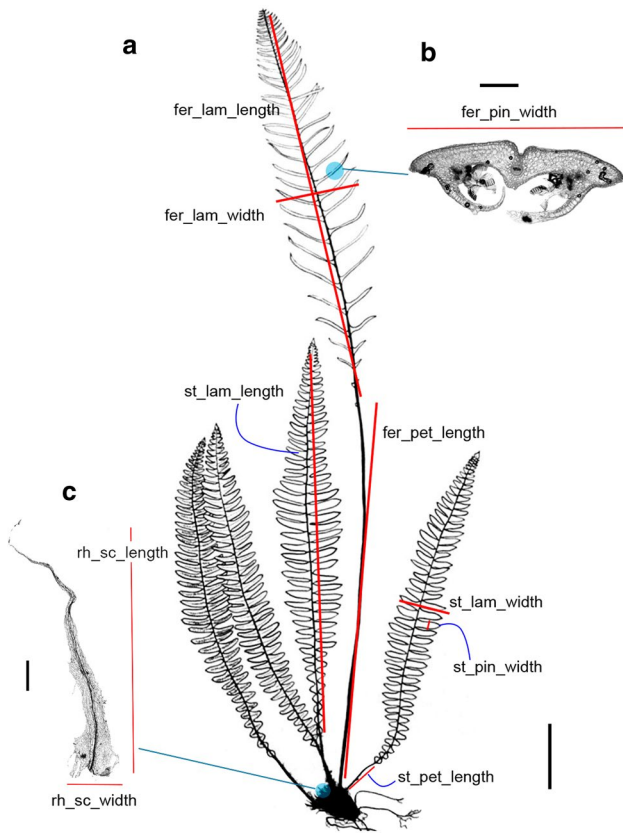


Fig. 3 Schematic of the traits observed. **a** Macromorphological variables regarding general sizes of both types of leaves. **b** Micromorphological variables regarding sizes of pinnae. **c** Micromorphological variables regarding sizes of rhizome scales. Refer to Table 1 for more detailed information on the names of the variables. Bar = 5 cm in **a**; 375 μ m in **b**; 800 μ m in **c**

complex (Table 1). One of these varieties, var. *pradae*, is newly recognized here on the basis of these data (see below).

For characters related to rhizome scales, the width of the base differed significantly between var. *fallax* and var. *pradae*, while var. *homophyllum* and var. *spicant* overlapped with each other and one of the other two varieties (Table 1). The length of the rhizome scales differed significantly between three groups: *S. spicant* var. *fallax* had the shortest scales, var. *homophyllum* had scales of intermediate length, and var. *spicant* and var. *pradae* had the longest scales. Besides these quantitative differences, qualitative differences exist as well (Fig. 4, Table 2). *Struthiopteris spicant* var. *spicant* has bicolorous (dark brown and pale brown), linear-lanceolate scales, with the middle section narrowly sclerosed from the base to the apex, entire margins, and flagelliform apex. Sometimes simple, pluricellular, uniseriate, and glandular hairs can be found on the margins of the scale. *Struthiopteris spicant* var. *pradae* has scales with the same characteristics as var. *spicant*. In contrast, var. *homophyllum* has concolorous (pale brown), triangular scales,

with the middle part almost not sclerosed, entire margins, and flagelliform apex. *Struthiopteris spicant* var. *fallax* has scales similar to those of var. *homophyllum*, that are lanceolate, concolorous (pale brown), without a sclerosed middle section, entire margins, and flagelliform apex.

Regarding the frond characters, we can distinguish two groups of taxa, one composed of *S. spicant* var. *fallax* and var. *homophyllum*, which have significantly shorter fronds, and the other by *S. spicant* var. *spicant* and var. *pradae*, which have significantly larger fronds (Tables 1, 2). In the case of some variables, such as sterile and fertile lamina width and sterile pinna width, the group *homophyllum* + *fallax* splits into two further, statistically significant groups, with *fallax* having the smaller dimensions. The trait “length of fertile laminae” differs significantly among all four taxa with var. *pradae* having the largest laminae, followed by var. *spicant*, var. *homophyllum*, and finally var. *fallax*.

The ratios calculated for the lamina dimensions also differ between taxa. The fertile lamina/petiole length ratio forms two groups, one with *S. spicant* var. *homophyllum* and var. *fallax*, which do not elongate the petioles in the fertile fronds, and the other group with var. *spicant* and var. *pradae*, which do so. The width of sterile pinnae/fertile pinnae ratio also formed two significantly different taxon groups, one with *S. spicant* var. *fallax* (monomorphic), and the other with var. *spicant* and var. *pradae* (dimorphic). *Struthiopteris spicant* var. *homophyllum* overlaps both groups (subdimorphic).

Struthiopteris spicant var. *pradae* has a second type of sporophyll with the same general appearance as the trophophyll. We measured 10 of these fronds, but did not include their measurements in the table since there is no equivalent frond type in the other varieties. The results for those fronds were laminae 30.14 (\pm 13.33) cm long, 4.36 (\pm 1.29) cm wide, petioles 10.66 (\pm 9.46) cm long, and pinnae 0.31 (\pm 0.09) cm wide.

The spore length character again discerned two groups of taxa, one with shorter spores formed by *S. spicant* var. *homophyllum* and var. *fallax*, and another with larger spores formed by *S. spicant* var. *spicant* and var. *pradae*. For spore width, there is a group formed by var. *homophyllum* and var. *fallax*, with narrower spores, another one with var. *spicant* and wider spores, and var. *pradae* overlapping both groups.

We carried out a principal components analysis on a data matrix containing the data from measurements of the fronds and rhizome scales. Factor loadings for each variable in each component are shown in Table 2. Three components explained 75.67% of the variance among taxa (Fig. 5). The PCA results (Fig. 5a, b) show that two major groups can be identified: one formed by three overlapping taxa, *S. spicant* var. *spicant*, var. *pradae*, and var. *homophyllum*, and another group formed by *S. spicant* var. *fallax*, which is clearly different from the rest of the taxa studied. When only components 2 and 3 are considered (Fig. 5c), there is a general

Table 1 Morphological traits measured in the four varieties within the complex *Struthiopteris spicant*. Values are expressed as mean \pm standard deviation, followed by number of samples measured in parentheses. Taxa with the same letter after the parenthesis for a particular variable show no statistical differences, as detected by a post hoc Tukey ANOVA ($\alpha=0.05$)

	<i>S. spicant</i> var. <i>fallax</i>	<i>S. spicant</i> var. <i>homophyllum</i>	<i>S. spicant</i> var. <i>spicant</i>	<i>S. spicant</i> var. <i>pradae</i>
<i>Traits relating to laminae/fronds</i>				
st_lam_length [cm]	1.55 \pm 0.31 (4)a	7.49 \pm 1.42 (13)a	21.46 \pm 6.18 (67)b	26.56 \pm 10.98 (25)b
st_lam_width [cm]	0.5 \pm 0.08 (4)a	1.62 \pm 0.86 (13)b	3.12 \pm 0.93 (67)c	3.52 \pm 1.24 (25)c
st_pet_length [cm]	0.23 \pm 0.13 (4)a	1.15 \pm 0.86 (13)a	4.93 \pm 2.88 (67)b	6.17 \pm 5.84 (25)b
st_pin_width [cm]	0.16 \pm 0.05 (4)a	0.29 \pm 0.09 (13)b	0.37 \pm 0.73 (67)bc	0.39 \pm 0.09 (25)c
fer_lam_length [cm]	2.8 \pm 1.36 (4)a	11.26 \pm 2.85 (24)b	28.35 \pm 9.82 (40)c	39.01 \pm 13.6 (8)d
fer_lam_width [cm]	0.75 \pm 0.16 (4)a	2.12 \pm 0.55 (24)b	4.04 \pm 1.35 (40)c	4.81 \pm 1.07 (8)c
fer_pet_length [cm]	0.45 \pm 0.34 (4)a	2.47 \pm 1.71 (24)a	10.91 \pm 4.77 (40)b	14.58 \pm 7.95 (8)b
fer_lam/pet_length	0.16 \pm 0.09 (4)a	0.21 \pm 0.55 (24)a	0.39 \pm 0.17 (40)b	0.37 \pm 0.15 (8)b
fer_pin_width [cm]	0.17 \pm 0.08 (4)a	0.2 \pm 0.05 (24)a	0.17 \pm 0.04 (40)a	0.18 \pm 0.05 (8)a
st_pin/fer_pin	1.04 \pm 0.67 (4)a	0.78 \pm 0.7 (13)ab	0.42 \pm 0.16 (40)b	0.4 \pm 0.15 (8)b
<i>Traits relating to rhizomes</i>				
rh_sc_length [μ m]	1705 \pm 272.03 (6)a	3609.72 \pm 980.39 (27)b	5581.14 \pm 2029.11 (57)c	6391.67 \pm 1236.93 (30)c
rh_sc_width [μ m]	408.33 \pm 148.88 (6)a	737.04 \pm 200.4 (27)ab	1673.68 \pm 454.34 (57)ab	971.25 \pm 316.89 (30)b
<i>Traits relating to spores</i>				
spore_length [μ m]	43.33 \pm 7.05 (60)a	37.93 \pm 4.79 (98)b	40.54 \pm 3.27 (59)c	42.33 \pm 5.24 (150)c
spore_width [μ m]	31.83 \pm 6.24 (60)a	26.56 \pm 4.45 (98)b	28.61 \pm 3.63 (59)c	29.43 \pm 3.31 (150)ac

Key to variable names: *st_lam_length* length of the sterile laminae, *st_lam_width* width of the sterile laminae, *st_pet_length* length of the sterile petiole, *st_pin_width* width of the sterile pinnae, *fer_lam_length* length of the fertile laminae, *fer_lam_width* width of the fertile laminae, *fer_pet_length* length of the fertile petiole, *fer_lam/pet_length* ratio of fertile laminae length/fertile petiole length, *fer_pin_width* width of the fertile pinnae, *st_pin/fer_pin* ratio of sterile pinnae width/fertile pinnae width, *rh_sc_length* length of the rhizome scale, *rh_sc_width* width of the rhizome scale, *spore_length* length of the spore, and *spore_width* width of the spore

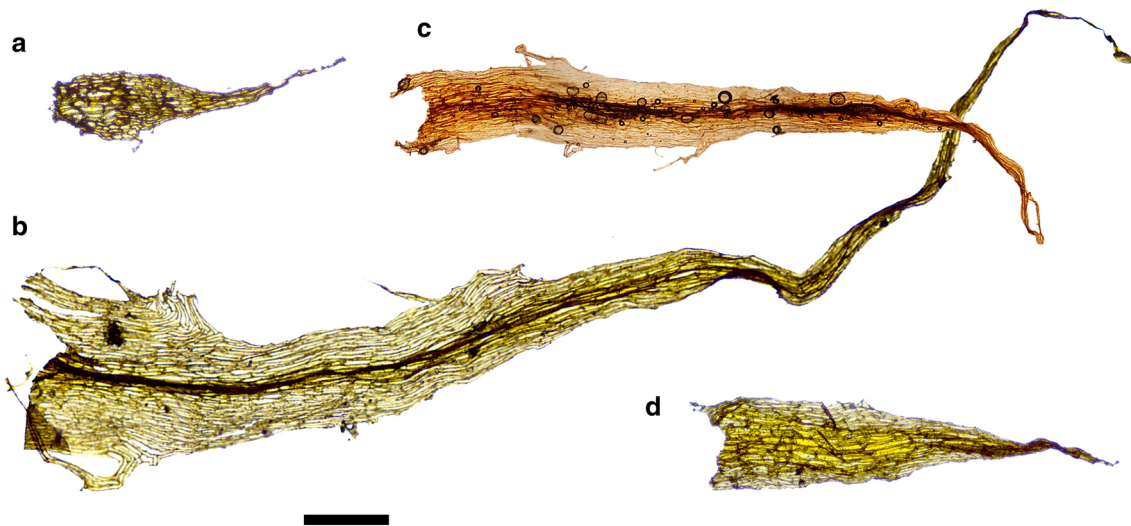


Fig. 4 Rhizome scales in taxa of the *Struthiopteris spicant* complex: **a** *S. spicant* var. *fallax*, **b** *S. spicant* var. *spicant*, **c** *S. spicant* var. *pradae*, **d** *S. spicant* var. *homophyllum*. Bar = 500 μ m

overlap of all taxa. This can be explained by the width of the rhizome scales and width of fertile pinnae, and variables that do not differ significantly between groups in the ANOVA.

Regarding anatomical sections of the pinnae (Fig. 6, Table 3), *S. spicant* var. *spicant* possesses fertile pinnae

which are contracted compared to the sterile pinnae, and with the margins slightly curved towards the abaxial side. The indusia are complex and thick (Fig. 6a). *Struthiopteris spicant* var. *fallax* is a monomorphic plant, so its fertile pinnae have similar anatomical features to the sterile ones,

Table 2 Morphological variables of the complex *Struthiopteris spicant* used in the PCA with the factor loadings for each component. For variable explanations see Table 1

	Component		
	1	2	3
st_lam_length	0.155	0.030	0.108
st_pet_length	0.129	0.031	0.071
st_lam_width	0.151	-0.017	0.010
st_pin_width	0.119	-0.130	-0.162
fer_lam_length	0.143	0.058	0.290
fer_pet_length	0.153	0.004	0.043
st_pet_length	0.135	0.096	0.224
fer_pin_width	-0.006	0.428	0.201
fer_lam/pet_length	0.097	-0.078	-0.257
st_pin/fer_pin	-0.075	0.376	0.285
rh_sc_width	-0.004	-0.317	0.637
rh_sc_length	0.109	0.225	-0.334

and indeed most fronds are fertile (Fig. 6b). *Struthiopteris spicant* var. *pradae* has the same characteristics as var. *spicant* for its standard sporophyll, but in addition it possesses a second type of sporophyll which is straighter, more like the trophophyll, and with a shorter indusium compared to the fully fertile pinnae (Fig. 6c). *Struthiopteris spicant* var. *homophyllum* has shorter indusia, and its fertile pinnae are similar than the sterile ones, due to their subdimorphic condition (Fig. 6d). In *S. s.* var. *spicant*, the pinnae are not curved in section, so the margins appear almost aligned with the meristele (Fig. 6a), whereas the margins are slightly curved in var. *homophyllum* (Fig. 6d) and var. *pradae* (Fig. 6c) (i.e. the margins are slightly displaced towards the abaxial surface from the plane of the meristele). Pinnae appear strongly curved in the case of *S. spicant* var. *fallax* (Fig. 6b), with the margins very displaced towards the abaxial surface from the plane of the meristele.

The epidermis in all taxa shares the following features: the stomata are arranged following the veins, and simple, pluricellular, uniseriate and glandular hairs are present on both abaxial and adaxial surfaces, as well as on the rachis. Some differences

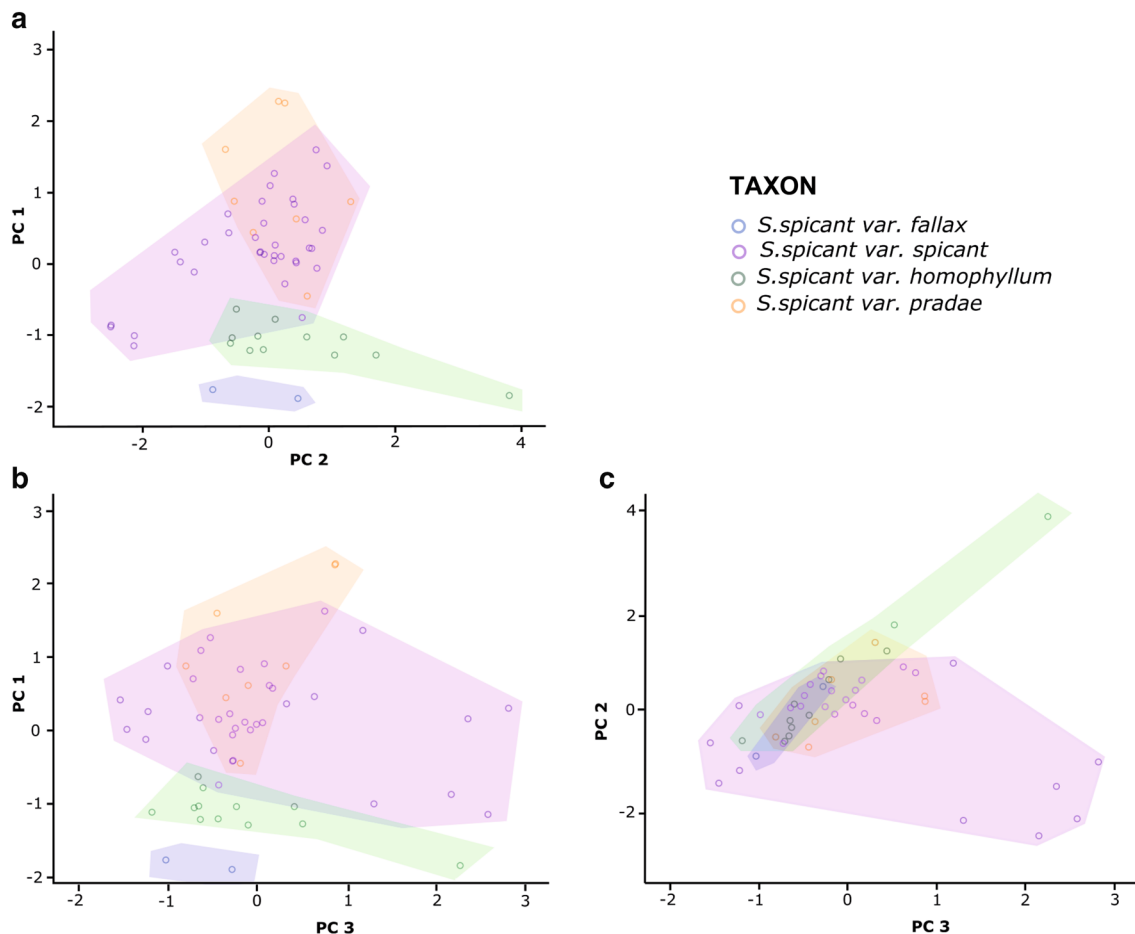


Fig. 5 Dispersal graphics of the three components resulted from the PCA labelled by taxon. **a** Component 1 versus component 2; **b** Component 1 versus component 3; **c** Component 2 versus component 3

Fig. 6 Anatomical sections of pinnae in taxa of the *Struthiopteris spicant* complex. The left column shows photographs of sections of fertile pinnae; the black lines pass through the middle of the meristele in each case and serve as a reference for the degree of abaxial displacement of the pinna margins. The right column shows schematic drawings comparing the width of sterile pinnae (above) and fertile pinnae (below) for each taxon. **a** Strongly dimorphic var. *spicant*, with margins not or only slightly displaced. **b** Monomorphic *S. spicant* var. *fallax*, with margins strongly displaced. **c** Strongly dimorphic var. *pradae*, with two types of fertile pinnae: uncontracted (right column middle drawing) and contracted (right column lower drawing); margins are somewhat displaced. **d** Subdimorphic var. *homophyllum* with margins somewhat displaced. Bar = 250 μ m in photographs, 450 μ m in schematic drawings

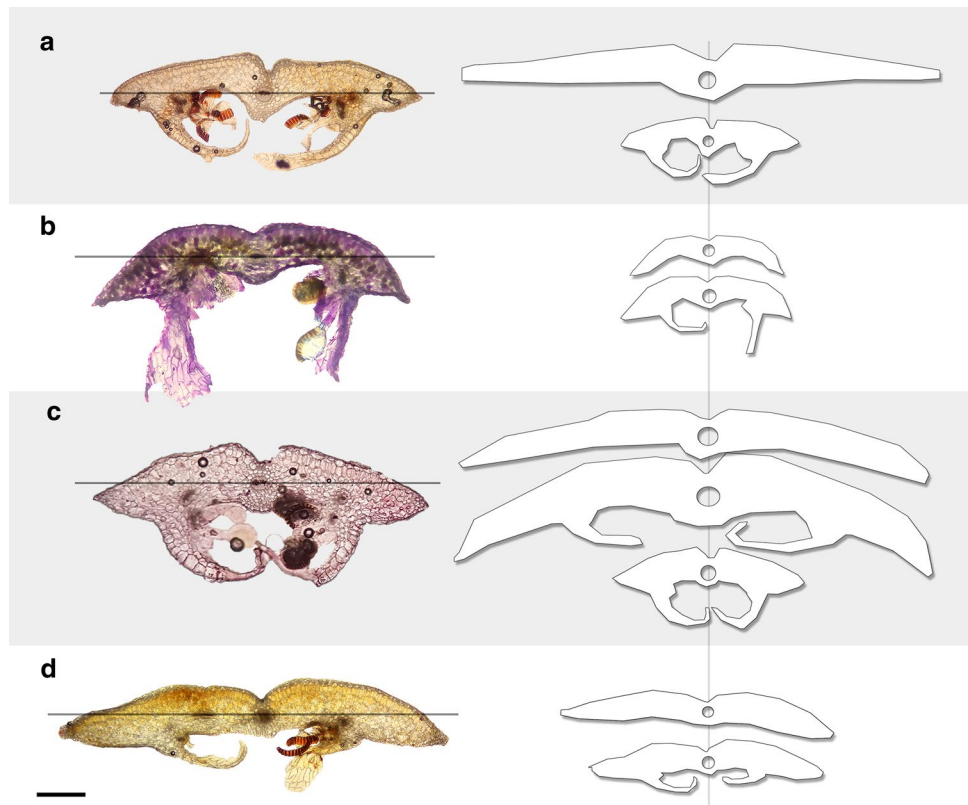


Table 3 Summary of the main morphological and anatomical features distinguishing the different taxa in the *Struthiopteris spicant* complex

	<i>S. spicant</i> var. <i>spicant</i>	<i>S. spicant</i> var. <i>homophyllum</i>	<i>S. spicant</i> var. <i>pradae</i>	<i>S. spicant</i> var. <i>fallax</i>
Rhizome scales	Linear-lanceolate, bicolorous	Triangular, concolorous	Linear-lanceolate, bicolorous	Lanceolate, concolorous
Frond dimorphism	Dimorphic	Subdimorphic	Dimorphic (with two types of sporophylls)	Monomorphic
Laminae length	Normally more than 20 cm	No more than 20 cm	Normally more than 20 cm	No more than 5 cm
Epidermis	Anticlinal walls strongly undulated	Anticlinal walls strongly undulated	Anticlinal walls strongly undulated	Anticlinal walls slightly undulated

were also observed in the epidermis cells and stomatal pattern (Fig. 7) as follows: in both the abaxial and the adaxial surfaces, the epidermis of *S. spicant* var. *fallax* possesses rectangular cells with anticlinal walls that are slightly undulated, and rounded stomata with narrower companion cells that are sometimes shared by more than one stomata. The remaining taxa share an epidermal pattern that differs notably from *S. spicant* var. *fallax*. The abaxial and adaxial epidermis have elongated cells with highly undulated anticlinal walls and ellipsoidal stomata with the same disposition as in (but larger than) *S. spicant* var. *fallax*.

Proposal of a new status for *Struthiopteris spicant* var. *fallax*

Struthiopteris spicant var. *fallax* is a unique plant. Its general morphology makes it highly probable that it belongs to the *S. spicant* complex, but several characters set it apart, including: a) traits regarding sterile reproductive structures are quite different from those in var. *spicant* (e.g. size and morphology of the rhizome scales, overall size of the plant, monomorphic fronds, anatomy of the pinnae and epidermis, and size of the spores); b) it has

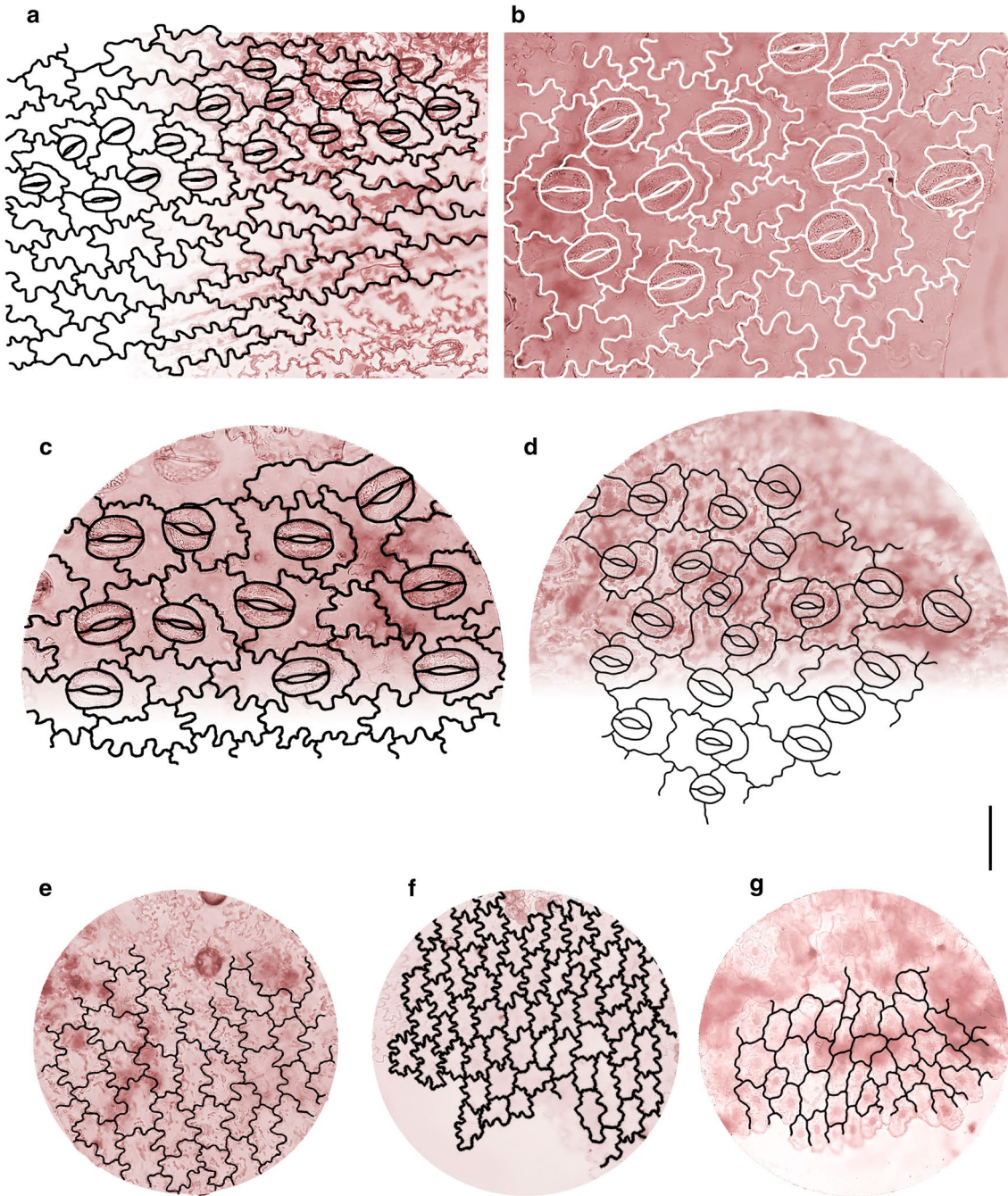
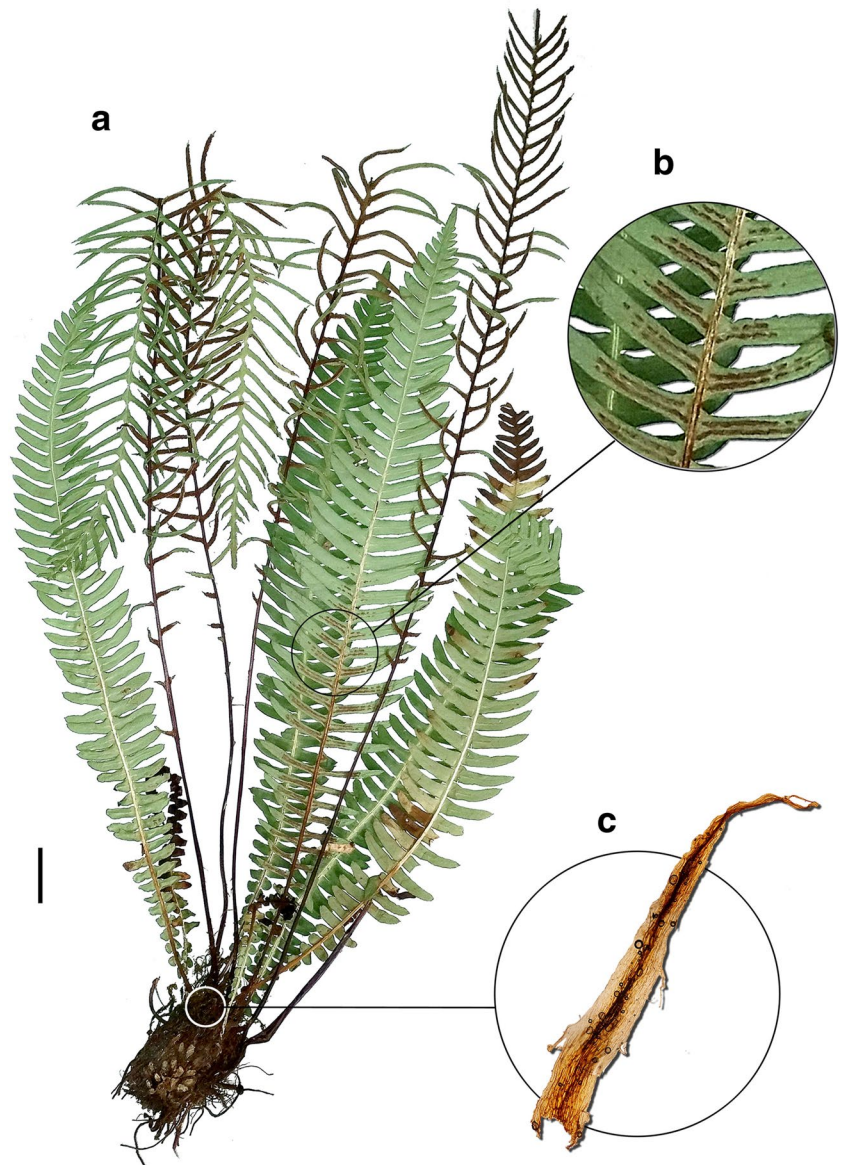


Fig. 7 Epidermal patterns in abaxial (a–d) and adaxial (e–g) leaf surfaces of members of the *Struthiopteris spicant* complex: **a** *S. spicant* var. *spicant*; **b**, *S. spicant* var. *homophyllum*; **c**, *f* *S. spicant* var. *pradae*; **d**, *g* *S. spicant* var. *fallax*. Bar = 80 μ m in a–d, 100 μ m in e–g

an isolated, highly localized distribution, occurring only near hot springs in Iceland; and c) it has a very particular ecology, related to its geothermal environment. Thus, although var. *spicant* also occurs in Iceland, populations of these two entities are ecologically well differentiated and their niches never overlap. As a result, intermediate, potentially hybrid plants between var. *spicant* and var. *fallax*

have never been detected, contrary to what occurs between var. *spicant* and the rest of the varieties considered in this work. In consequence, it seems to us that var. *fallax* can be better seen as a geographically and ecologically isolated lineage, which falls completely within the concept of a unique species. The formal taxonomic treatment is presented below.

Fig. 8 Holotype of *Struthiopteris spicant* var. *pradae*, MACB 110654. **a** Individual showing the typical three types of fronds. **b** Detail of the sporogenous area of the short fertile frond, with plain, uncontracted pinnae and interrupted sori. **c** Rhizome scale. Bar = 2 cm in **a**, 0.7 cm in **b**, 650 μ m in **c**



Description of a new variety in *Struthiopteris spicant*

Plants with sterile fronds and two distinct types of fertile fronds were found in several localities in the north of the Iberian Peninsula. Young individuals bear several fronds that resemble typical “sterile *spicant*” fronds, most of which are sterile but one or two of which are at least partially sporogenous, non-contracted, and with interrupted sori and indusia. Mature individuals develop, in addition to these two frond types, at least one fully sporogenous frond that resembles the typical “fertile *spicant*” frond, with highly contracted pinnae and continuous cenosori (Fig. 8). Spores from both types of sporophylls appear morphologically sound and fertile.

Plants with this unique three-frond morphology have been located to date in four different and distant localities (Fig. 9). One has been visited continuously for 3 years, and new plants with this form were always detected, ranging from small, young individuals to large, older ones.

The general appearance and almost all the morphological details undoubtedly bring this plant into *S. spicant*. However, the constant presence of the characteristic third type of partially sporogenic leaf with flat pinnae in individuals from populations that are distant from one another and persistent in time suggests that these populations represent a race that can be considered as different from the typical form of *S. spicant*. In consequence, we proceed here to name and describe this race as a new variety. The formal taxonomic treatment is presented below.

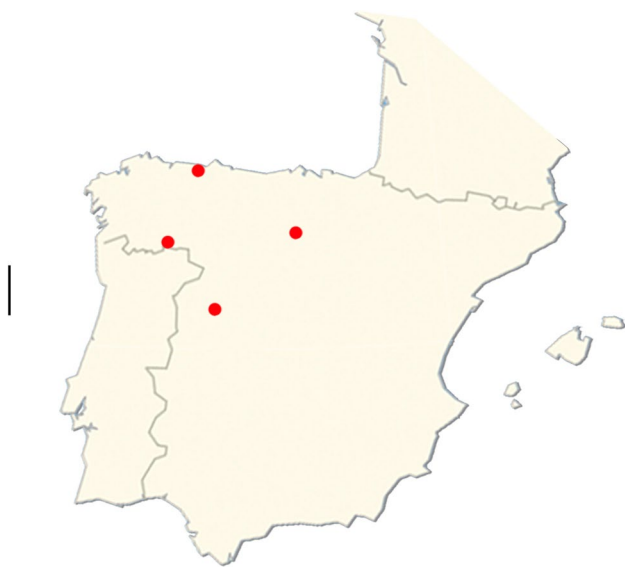


Fig. 9 Distribution map of *Struthiopteris spicant* var. *pradae*, showing the four distant known localities in northern Spain. Bar = 100 km

Discussion

While differences in the shape and size of fronds have previously been reported in *S. spicant* var. *homophyllum* and *S. fallax* (Merino 1898; Löve and Löve 1966; Ormonde 1986; Wasowicz et al. 2017b), in the current work we present the first statistical support for such differences based on ANOVA and principal components analyses that distinguish clear groups within the taxa studied. It is clear from our data and analyses that the general morphology and the size of the fronds are crucial characters to distinguish *S. fallax* and all the taxa within the *S. spicant* complex. In the case of *S. fallax*, its size, degree of dimorphism, and isolated location support its elevation to the species level, and in the case of the new variety *S. spicant* var. *pradae*, the presence of a unique second type of sporophyll sets it apart.

Rhizome scales are structures widely used by fern taxonomists and are particularly important in the Blechnaceae (Kramer et al. 1990; Rolleri and Prada 2006; Rothfels et al. 2012) to discriminate genera and species. In this study, the rhizome scales observed in *S. spicant* var. *spicant* agree with a previous work (Rolleri and Prada 2006) except for the description of the margins, which are described as dentate in that study but entire in this work. Rolleri and Prada (2006) studied just three individuals, while we have examined more than 30, so the discrepancy in our observations may be due to differences in sampling. In the rest of the taxa, the rhizome scales have not been described before, and we demonstrate that they are useful for distinguishing these taxa in the case of *S. spicant* var. *homophyllum*, var. *spicant*, and *S. fallax* (Table 1).

Spores are another extremely important character for classifications in ferns (Tryon and Lugardon 1991). The spores of *S. spicant* var. *spicant* have been described in several studies, and those previous descriptions agree well with the characteristics found in this work (Lugardon 1965, 1974; Tryon and Lugardon 1991; Rolleri and Prada 2006; Passarelli 2007; Passarelli et al. 2010). Ours are the first data reported for the remaining taxa, and we find significant differences in spore size between several taxa (Table 1). Since differences in size have been found for *S. spicant* var. *homophyllum* and *S. fallax* compared to *S. spicant* var. *spicant*, it would be interesting to carry out a more detailed study of additional characters of perispore morphology to determine whether further traits exist that would be useful to discriminate these entities.

Cross sections of pinnae have also proved very informative and offer valuable characters to separate genera and even species in the family Blechnaceae (Prada et al. 2016; Vicent 2017). Previous studies have described the anatomy and associated structures to the fertile pinnae for *S. spicant* var. *spicant*, which agree with our observations here. We also present the first pinnae cross sections for the remaining taxa in the complex and show their utility to distinguish them (Table 1, Fig. 6).

The morphology of the epidermis is another character newly described here for all the entities in this study except for *S. spicant* var. *spicant*, which has been already described (Rolleri and Prada 2006) and whose main characteristics agree with the data reported in this study. The chief differences we identified pertain primarily to *S. fallax*, which has cell walls only slightly undulating compared to the remaining taxa we considered (Table 2, Fig. 7), and which constitutes one piece of evidence supporting its separation from the *S. spicant* complex.

Regarding the new status of *S. fallax*, even though its general morphology and chromosome number (Löve and Löve 1968) would equally well support that this taxon is part of the *S. spicant* complex, we have also considered the following facts: a) we reported in this study a number of characters that are significantly different from *S. spicant* (including general macromorphology, rhizome scales, pinnae anatomy, and cells of the epidermis); b) there is a hard ecological boundary between the two taxa and as a result their niches and local habitat never overlap (in Iceland *S. spicant* is most common in snowbeds and ravines, while *S. fallax* is confined to high-temperature geothermal areas); c) the presence of intermediate individuals between *S. spicant* and *S. fallax* has never been confirmed (Wasowicz et al. 2017b); and d) when cultivated far from its natural distribution area, *S. fallax* preserves the same morphological characteristics and does not begin to resemble *S. spicant* (Löve and Löve 1968). For all of these reasons, we raise this taxon to the level of species

and find it plausible that it could be a close relative of var. *spicant* that has become adapted to hot springs.

We also propose a formal status for *S. spicant* var. *pradae*, based mainly on the presence of two type of sporogenous fronds in addition to the normal sterile ones, as noted above, a distinct morphology that merits taxonomic recognition. The presence of two distinct types of fertile fronds could led to the consideration that the plant is trimorphic, but this is not necessarily the case and deserves some explanation. Pteridologists describe a fern as dimorphic when there is a distinction between sporophylls and trophophylls (Wagner and Wagner 1977). The term is often used somewhat informally to acknowledge this characteristic, because it is recognized that dimorphism “*may sometimes apply to other than fertile-sterile (i.e., various types of heterophylly of vegetative leaves in ferns)...*”, and is somewhat arbitrary “*because of so many transitions that occur between monomorphy and dimorphy*” (*op. cit.*, p. 251).

True dimorphism in leaves is a common feature in ferns, and occurs in as many as 20% of fern species belonging to many genera of phylogenetically unrelated families (Watkins et al. 2016). In dimorphic ferns, the two types of fronds differ in morphology in ways associated with their different functions. Typically, the sterile leaf develops with an expanded, well-developed lamina for photosynthesis, while the fertile type has heavily contracted, sporogenous pinnae that lack green tissue when mature. Truly trimorphic ferns are much more unusual, and only a handful of cases have been documented, mainly falling into the category that Wagner and Wagner (1977) cite as “heterophylly of vegetative leaves”. In these species, besides the presence of sporogenous, morphologically different fronds, there are two types of sterile ones. The best studied cases are those of some climbing species, which can develop smaller or simpler fronds when in contact with soil but produce very much larger and more divided fronds when in contact with the tree host as for example the Blechnaceae species *Icarus filiformis* (A.Cunn.) Gasper & Salino (Breitwieser et al. 2010–2018). *Austroblechnum asperum* (Klotzsch) Gasper & V.A.O.Dittrich (Blechnaceae) produces long, creeping, stoloniferous sterile fronds with very reduced lobes (Rodríguez-Ríos 1995) but the contracted fertile fronds are very short, which is intriguing because sporogenous fronds are expected to be tall in order to help spreading the spores. In *Platyzoma microphyllum* R.Br. (Pteridaceae) a set of highly reduced, small, filiform fronds are produced at the base of the normal ones (Tryon and Tryon 1982); the function of these, if any, remains unknown.

In contrast to these “trimorphic” ferns with two types of sterile leaves, little has been written or observed about ferns with two types of fertile fronds. Wagner and Wagner (1977) stated that the emergence of distinct fertile

fronds could be a gradual process, and that the manifestations of dimorphism is transitional: thus, for many ferns, “*many fertile fronds are merely “subdimorphic” in the sense that the changes displayed are incomplete in kinds and amounts*”. This describes the case of plants like *S. spicant* var. *pradae* well. This taxon and others previously documented, such as some members of the polypodiaceous genus *Pyrrosia* Mirb. (Hovenkamp 1986), are essentially different from both dimorphic and trimorphic ferns. Strictly speaking, we cannot consider this a case of true dimorphism or trimorphism, but a case somewhat intermediate between the two. This striking fact deserves further investigation to elucidate the status of such “pseudotrimorphic” ferns.

Taxonomic treatment

Identification key for the European taxa of *Struthiopteris*

- 1a Plants dimorphic or subdimorphic, > 5 cm tall 2
- 1b Plants monomorphic, < 5 cm tall. Iceland *S. fallax*
- 2a Rhizome scales lanceolate-triangular, concolour, rarely bicolour; plants subdimorphic, < 20 cm tall
..... *S. spicant* var. *homophyllum*
- 2b Rhizome scales linear, bicolour; plants dimorphic, usually > 20 cm tall 3
- 3a Plants with just one type of sporophyll
..... *S. spicant* var. *spicant*
- 3b Plants with two types of sporophylls
..... *S. spicant* var. *pradae*

Struthiopteris fallax (Lange) S.Molino, Gabriel y Galán & Wasowicz, **comb. & stat. nov.** ≡ *Blechnum spicant* var. *fallax* Lange, Fl. Dan. [Oeder] 17(fasc. 50): 11, t. 1988. 1880. ≡ *Struthiopteris spicant* var. *fallax* (Lange) Wasowicz & Gabriel y Galán, Phytotaxa 302: 198. 2017.—LECTOTYPE: Island, Tunguhver, varme Kilde, *Ch. Grønland s.n.* (designated in Wasowicz et al. 2017a): C barcode C10021769, left hand specimen [n.v]).

Struthiopteris spicant var. *pradae* S. Molino & Gabriel y Galán, **var. nov.**—HOLOTYPE: **Spain**: Zamora, Aciberos, c. 3 km west from the village, in a shadowed slope near the road, under a canopy of *Fraxinus angustifolia* and *Quercus pyrenaica*, 42.038942°, –6.861643°, 1220 m a. s.l., 20 Sep 2017, Molino, Seral, de la Fuente and Gabriel y Galán (MACB10654) (Fig. 8).

Diagnosis: This variety differs from the typical var. *spicant* in having two types of fertile fronds, one that is larger than the sterile fronds and with contracted fertile pinnae, and at

least one that is the same size as the sterile fronds and whose pinnae are not contracted, thus completely resembling sterile fronds, except in being partially fertile.

Etymology: This variety is dedicated to renowned Spanish pteridologist Carmen Prada.

Habitats: It usually grows on wet slopes with siliceous soils.

Distribution area: The species is endemic to Spain and occurs in the north of the Iberian Peninsula, in the provinces of Zamora (near Puerto de Padornelo), Asturias (near Luarca), Salamanca (Sierra Peña de Francia), and Burgos (Sierra de la Demanda) (Fig. 9).

Additional specimens examined: See Appendix 1.

Conservation status: Although we do not have enough data to propose a specific status yet, we have detected just four populations of this plant and in none of them does the variety seem to be very abundant, so it may be a vulnerable or endangered taxon.

Acknowledgements The Universidad Complutense de Madrid partially supported this research through the funding of the research project PR26/16-20295 and a field trip to Iceland (International Mobility Program 2016).

Compliance with ethical standards

Conflict of interest The authors declare that they have not conflict of interest.

Human and animal rights This research did not involve any testing on humans or animals.

Appendix 1

List of materials in alphabetical order of taxa, with indication of location, voucher, and number of individuals per voucher.

Struthiopteris fallax (Lange) S. Molino, Gabriel y Galán & Wasowicz.

ICELAND Deildartunguhver, Wasowicz and Gabriel y Galán 7 Jul 2016, (MACB 109359) (3 individuals).

Struthiopteris spicant (L.) Weiss **var. *spicant***

AUSTRIA. Salzburg, Hohe Tauern, 20 Jul 1994, *Eberwein* and *Vitek* (MA 767022). **BELGIUM.** Turnhout, Engels Kamp park2, 18 Jun 1973, *W. Van Cotthem* (MA 809713). **FRANCE.** Sources Forest de l'Esterel, 01 Aug 1958, *G. Gavelle* (MA 186653). Serans (Oise), 22 Jul 1921, *P. Bossardet* (P 1001059). **ICELAND.** Vestfirðir, 8 Jul 2016, *Gabriel y Galán* and *Wasowicz* (MACB 110659). **IRELAND.** Iveragh,

Caherdaniel, 17 Jul 2016, *Molino* and *Pachón* (MACB 109619). **NORWAY.** Telemark, Nottoden, 15 Aug 2004, *P. Sunding* (MA 747921). **SPAIN. Asturias:** Valdés, Luarca, 12 Apr 2017, *Gabriel y Galán* (MACB 109615) (7 individuals). **Canary Islands:** Anaga, Tenerife, 25 Oct 1989, *Santos* (MACB 36152); Anaga, Tenerife, 14 Sep 2017, *Gabriel y Galán* (MACB 110658) (2 individuals). **Cantabria:** Camaleño, Cosgaya, 8 Oct 2016, *Gabriel y Galán* (MACB 109622) (4 individuals). **Madrid:** Dehesa de Somosierra, 31 May 2017, *Gabriel y Galán* and *Molino* (MACB 109611). **Zamora:** Aciberos, 23 Sep 2017, *Molino* et al. (MACB 110655). **Pontevedra:** Monte Aloya, Tuy, 15 Jul 1993, *Pajarón* and *Pangua* (MACB 59142). **UNITED KINGDOM.** South Somerset, Seven Wells Wood, 30 Jul 1968, *J.A. Crabbe* (MA 195093). Mid Ebudes, Mull, Tobermory, 06 Jul 1970, *Crabbe* and *Jermy* (MA 195091).

Struthiopteris spicant* var. *homophyllum (Merino) Gabriel y Galán & R.Pino

PORTUGAL. Braga, Vieira do Minho, 1 Oct 2004, *Prada* (MACB 109621). **SPAIN. La Coruña:** Santiago, Cantaleta, 29 Jul 1967, *Barrera* (MACB 32367). **Pontevedra:** between Tabagón y Tomiño, 19 Mar 2016, *Gabriel y Galán* (MACB 109617); Mondariz, 20 Mar 2016, *Gabriel y Galán* (MACB 109618). **Salamanca:** Batuecas, 15 May 2016, *Gabriel y Galán* (MACB 109626) (4 individuals).

Struthiopteris spicant* var. *pradae S.Molino & Gabriel y Galán

SPAIN. Asturias: Valdés, Paladeperre, 22 Mar 2016, *Gabriel y Galán* (MACB 109613) (3 individuals); 3 Aug 2016, *ibidem* (MACB 109615) (3 individuals); Luarca, 26 Jul 2017, *Gabriel y Galán* (MACB 110660); Otur, 17 Aug 2017, *Gabriel y Galán* (MACB 110661). **Burgos:** Sierra de San Millán, 27 Sep 1975, *Fuentes* (MACB 5994). **Salamanca:** San Miguel de Valero, 14 May 2016, *Gabriel y Galán* (MACB 109624) (3 individuals). **Zamora:** Aciberos, 23 Sep 2017, *Molino* et al. (MACB 110654).

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