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Monograph of the genera *Struthiopteris* Scop. and *Spicantopsis* Nakai (Blechnaceae, Polypodiopsida)

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ABSTRACT

The Blechnaceae fern family, comprising approximately 250 species, exhibits a subcosmopolitan distribution but showcases notable diversity in South America and the Austropacific region. Recent taxonomic revisions expanded the generic treatment within the family, Resulting, among other things, in the resurrection of the genus *Spicantopsis*. This genus, segregated from *Struthiopteris*, now encompasses three species endemic to East Asia. *Struthiopteris*, on the other hand, has three species distributed in Japan, Europe, North of Africa, and western North America. Molecular evidence, coupled with morphoanatomical traits, supported this taxonomic distinction. Despite subsequent studies on palynological and morphoanatomical characteristics, a comprehensive global monograph of *Struthiopteris* and *Spicantopsis* is lacking. This paper aims to fill this gap by synthesizing available information, providing identification keys, full descriptions, taxonomic notes, and some necessary type designation for all species within both genera. The study, based on the examination of 1,649 herbarium specimens and digital materials, underscores the importance of anatomical and morphological characters in fern taxonomy. Mapping distribution data further enhances understanding of the geographic ranges of these ferns. This comprehensive synthesis contributes to the ongoing elucidation of fern diversity and taxonomy.

Key words: *Blechnum*, ferns, neotype, taxonomy

INTRODUCTION

The Blechnaceae Newman (1844: 8) is a family of leptosporangiate ferns with about 250 species (Gasper *et al.* 2016, PPGI 2016). Although they exhibit subcosmopolitan distribution they have two main centers of diversity: South America and the Austropacific region (Kramer *et al.* 1990). The family underwent a drastic reclassification following the work of Gasper *et al.* (2016, 2017), whereby the generic treatment expanded from 9–10 genera to 24. Shortly thereafter a work by Molino *et al.* (2019b) resulted in the resurrection of one more genus, *Spicantopsis* Nakai (1933: 180), which was segregated from *Struthiopteris* Scopoli (1754: 25) based on morphoanatomical and molecular evidence.

Struthiopteris is a genus consisting of three species distributed in the northern hemisphere (Figure 1). The most widely distributed species is *Struthiopteris spicant* (Linnaeus 1753: 1066) Weiss (1770: 287), which occurs in Europe, North Africa, Macaronesian archipelagoes and the Pacific coast of North America, both in the United States and Canada (Figure 2). *Struthiopteris fallax* (Lange 1880: 11, t.1988) S. Molino, Gabriel y Galán & Wasowicz in Wasowicz *et al.* (2019b: 266), is endemic to a hot spring in Iceland (Figure 3). Finally, *Struthiopteris castanea* (Makino & Nemoto 1925: 1591) Nakai (1933: 186) is endemic to Japan (Figure 4). *Spicantopsis* is a genus endemic to East Asia (Figure 5) with three species: *Spicantopsis amabilis* (Makino 1897: 83) Nakai (1933: 184) and *Spicantopsis niponica* (Kunze 1848: 508) Nakai (1933: 181) endemic to Japan (Figures 6 and 7, respectively) and *Spicantopsis hancockii*

(Hance 1883: 267) Masamune (1936: 29) endemic to Taiwan (Figure 8) (Ebihara 2016, Molino *et al.* 2019b, Ebihara *et al.* 2023).

The genus *Spicantopsis* was first proposed by Nakai (1933), who segregated it from *Struthiopteris* considering the position of the stomata, which did not follow the veins in *S. amabilis*, *S. hancockii* and *S. niponica* but did in all other *Struthiopteris* species. Moreover, prior to this it had already been observed that the stomata pattern of development was different in these species (Kondo 1929). This view was rejected a few years later as this character was not considered sufficient to separate two different genera (Ching 1940, Tagawa 1952). However, later cytogenetic studies suggested that these species might belong to different groups, since *S. amabilis*, *S. hancockii* and *S. niponica* were diploid with $x = 31$ and *S. castanea* decaploid with $x = 34$ (Nakato 1987). This study suggested that *S. castanea* was more closely related to *S. spicant* and *S. fallax* with $x = 34$ (Löve & Löve 1968). Finally, Molino *et al.* (2019b) presented the first phylogeny including all six species, showing not only the existence of two well-delineated clades (one with *S. spicant*, *S. castanea* and *S. fallax* and another with *S. amabilis*, *S. hancockii* and *S. niponica*), but also the polyphyly of *Struthiopteris sensu* Gasper *et al.* (2016, 2017) after the inclusion of *Blechnidium melanopus* (Hooker 1860: 161) Moore (1860: 210). This, coupled with morphoanatomical evidence such as stipe color, presence of epidermal indumentum, shape of coenosori, anatomical profile of the fertile pinna and spore ornamentation led to resurrect the genus *Spicantopsis*, which has been adopted in other works as the TPG (2019).

Since this, works have been published concerning palynological characters of *Struthiopteris* and *Spicantopsis* (Molino *et al.* 2020) or morphoanatomy and distribution extensions of *Struthiopteris* (Molino *et al.* 2019a, c, 2021), but a proper global monograph of both genera has not yet been published. Therefore, in this paper we attempt to synthesize all the information available to date, presenting identification keys, descriptions, and taxonomic notes for all species of the genera *Struthiopteris* and *Spicantopsis*.

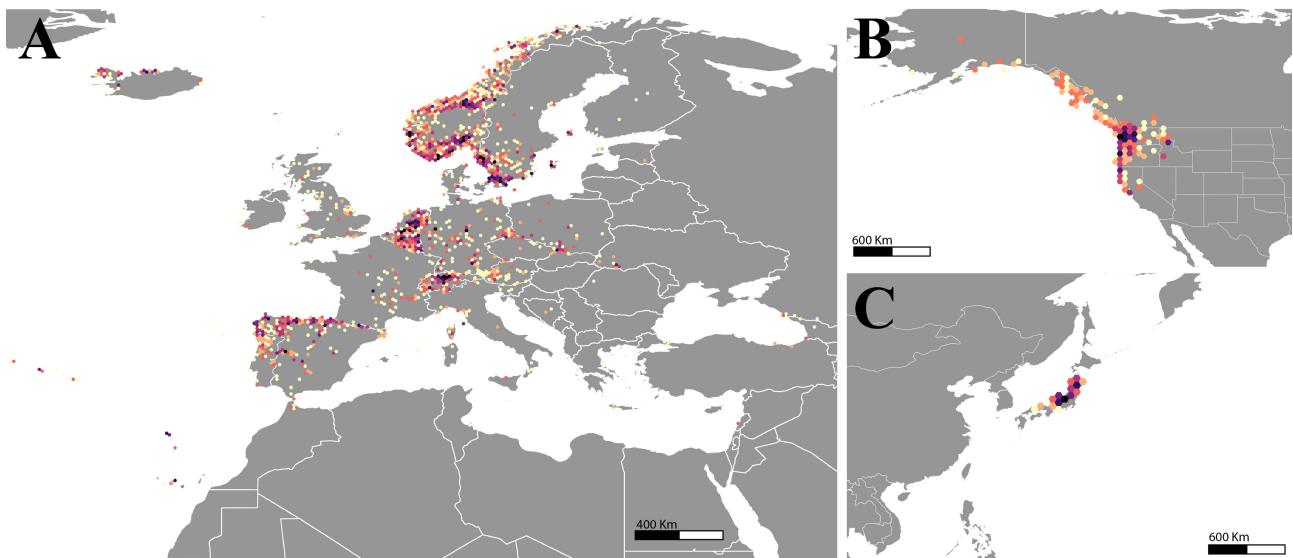


FIGURE 1. Distribution of *Struthiopteris* extracted from GBIF. The intensity of the color represents the lower (yellow) or higher (purple) density of occurrences. A. Distribution of *Struthiopteris* on Europe and North of Africa; B. Distribution of *Struthiopteris* on North America; C. Distribution of *Struthiopteris* on Japan.

Material and Methods

The study is based on the revision of 1,649 herbarium specimens of all *Struthiopteris* and *Spicantopsis* taxa. We examined specimens from the following institutions included in Index Herbariorum (Thiers 2024. Continuously updated): F, MA, MACB, MO, NY, P, S, TNS, and US, and we examined high-resolution digital material from specimens deposited at BISH, CHRB, GA, H, LINN, MAK, MICH, NCU, TAI, TAIF, TI, and U, accessed through the official webpages of the herbaria, GBIF (2024), JSTOR Global Plants (2023), and in PteridoPortal (2023). A relation of all studied specimens is listed after each taxon in the **taxonomic treatment** section. Additional images of the plants in the field have been consulted on PlantSystematics (2023) and iNaturalist (2023).

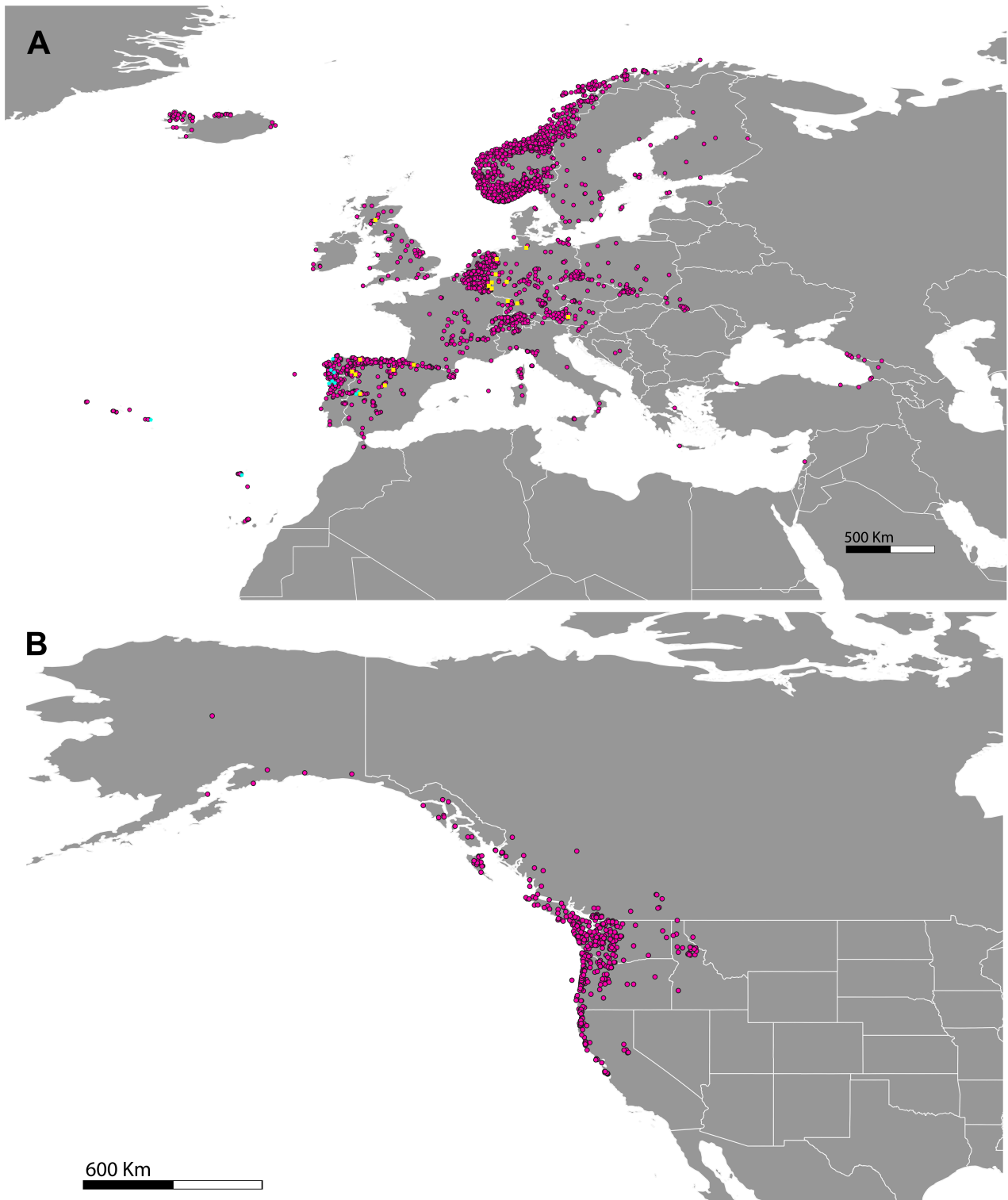


FIGURE 2. Distribution of *Struthiopteris spicant* extracted from GBIF. Purple circles: *Struthiopteris spicant* var. *spicant*; yellow squares: *Struthiopteris spicant* var. *pradae* (added manually); blue pentagons: *Struthiopteris spicant* var. *homophyllum* (added manually).

Nomenclature

Nomenclature followed the floristic treatments cited in the corresponding sections, complemented with the information present on IPNI (2023), Tropicos.org (2023), and Ebihara & Kasetani (2018). The backbone phylogeny of the genera *Struthiopteris* and *Spicantopsis* and the systematic starting point of this work is the one published by Molino *et al.* (2019b, c). Additional information on old publications, authors, and collectors was also gathered in BHL (2024), Bionomia (2023), and Botanicus (2023).

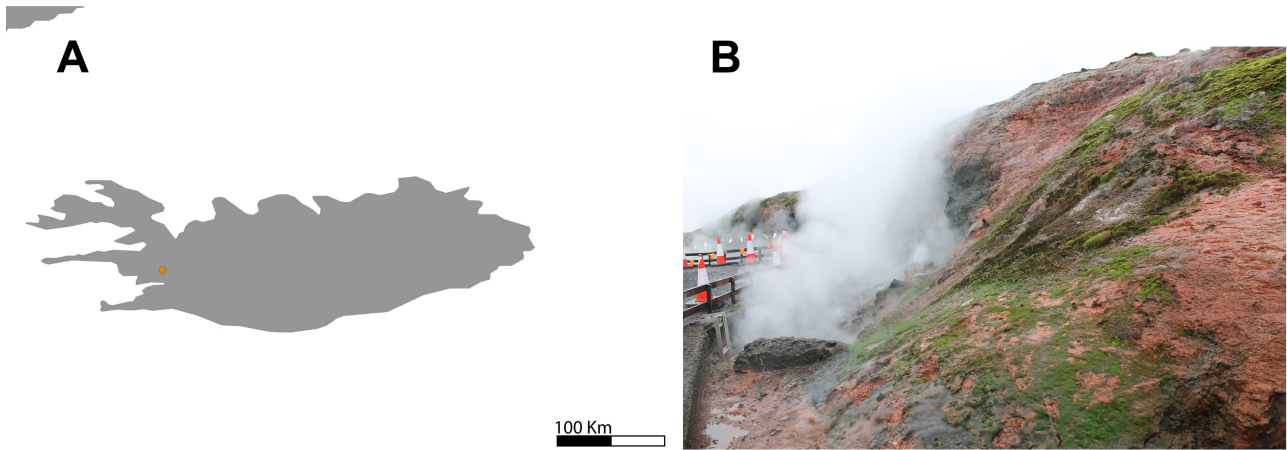


FIGURE 3. A. Distribution of *Struthiopteris fallax* at Deildartunguhver, Iceland (added manually); B. Habitat where *S. fallax* grows: slope next to the hot spring of Deildartunguhver (picture: Sonia Molino).

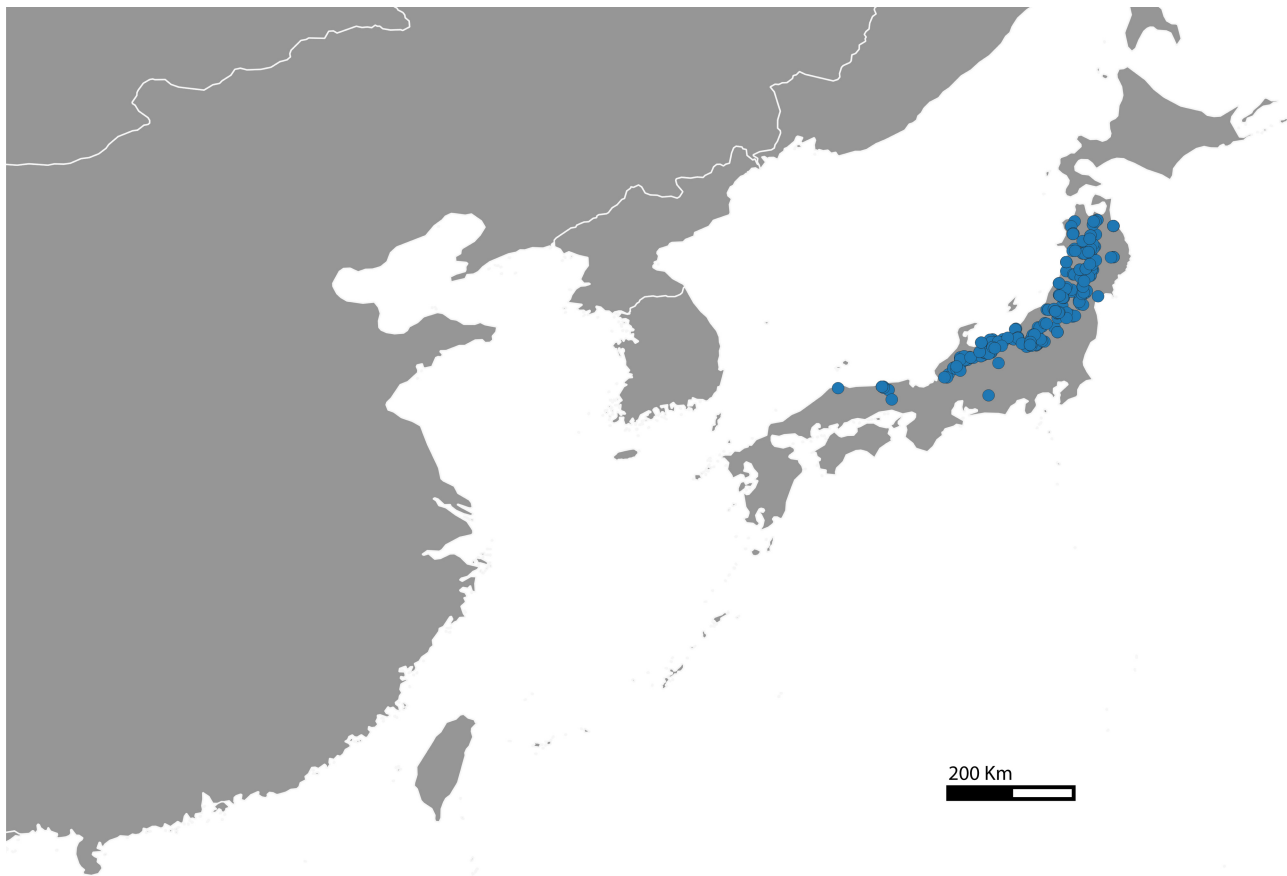


FIGURE 4. Distribution of *Struthiopteris castanea* extracted from GBIF.

We carried out a study of the general morphology of the plants (i.e. fronds, scales, rhizomes, epidermis etc.), for all specimens of *Struthiopteris* and *Spicantopsis* we could access. We also performed a study on anatomy of the fertile pinnae, sporangia and spores which has already been published (Molino *et al.* 2019b, c, 2020). Our character choice has already demonstrated a broad taxonomic usefulness in pteridology (e.g. Kramer *et al.* 1990) and in the Blechnaceae in particular (e.g. Rolleri & Prada 2006). For the terminology, we used Lellinger (2002).

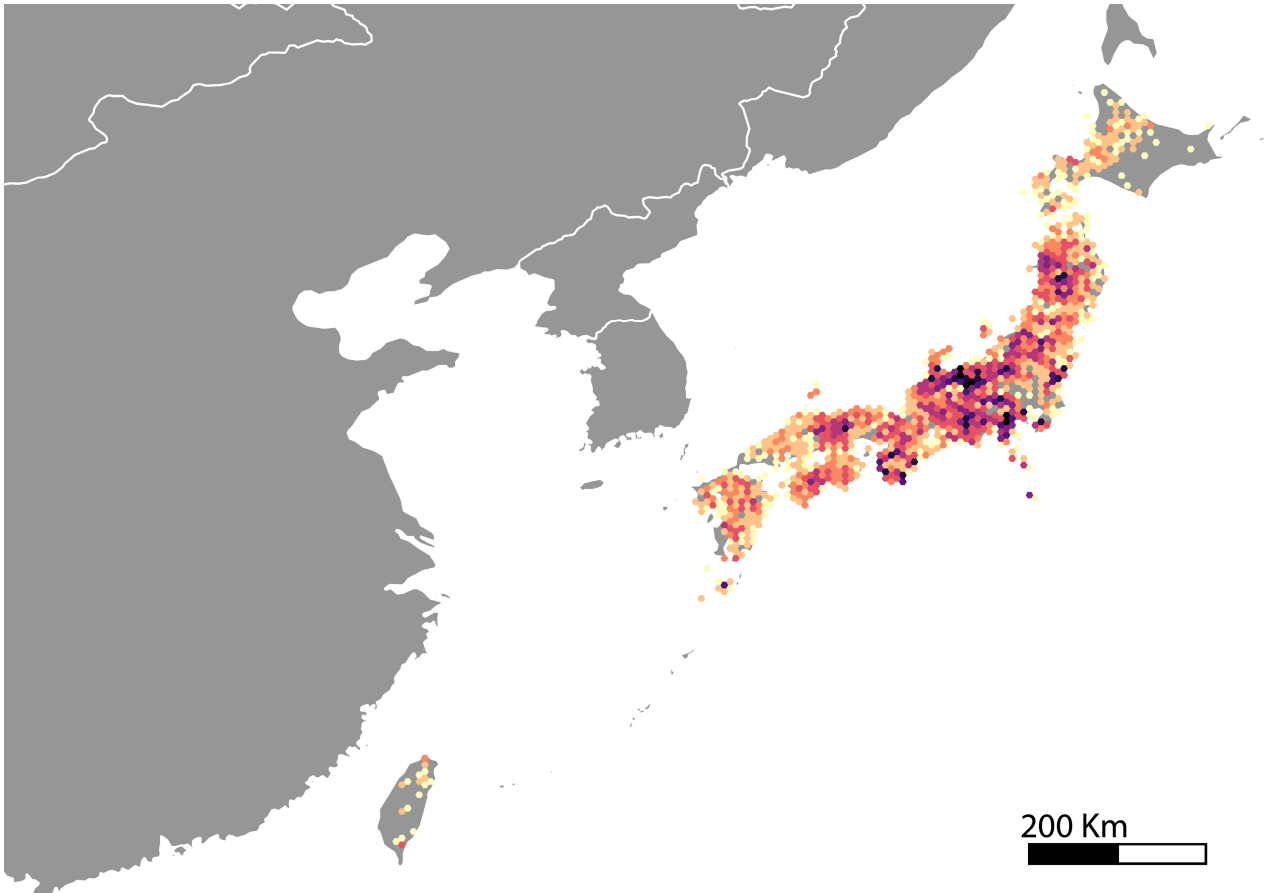


FIGURE 5. Distribution of *Spicantopsis* extracted from GBIF. The intensity of the color represents the lower (yellow) or higher (purple) density of occurrences.

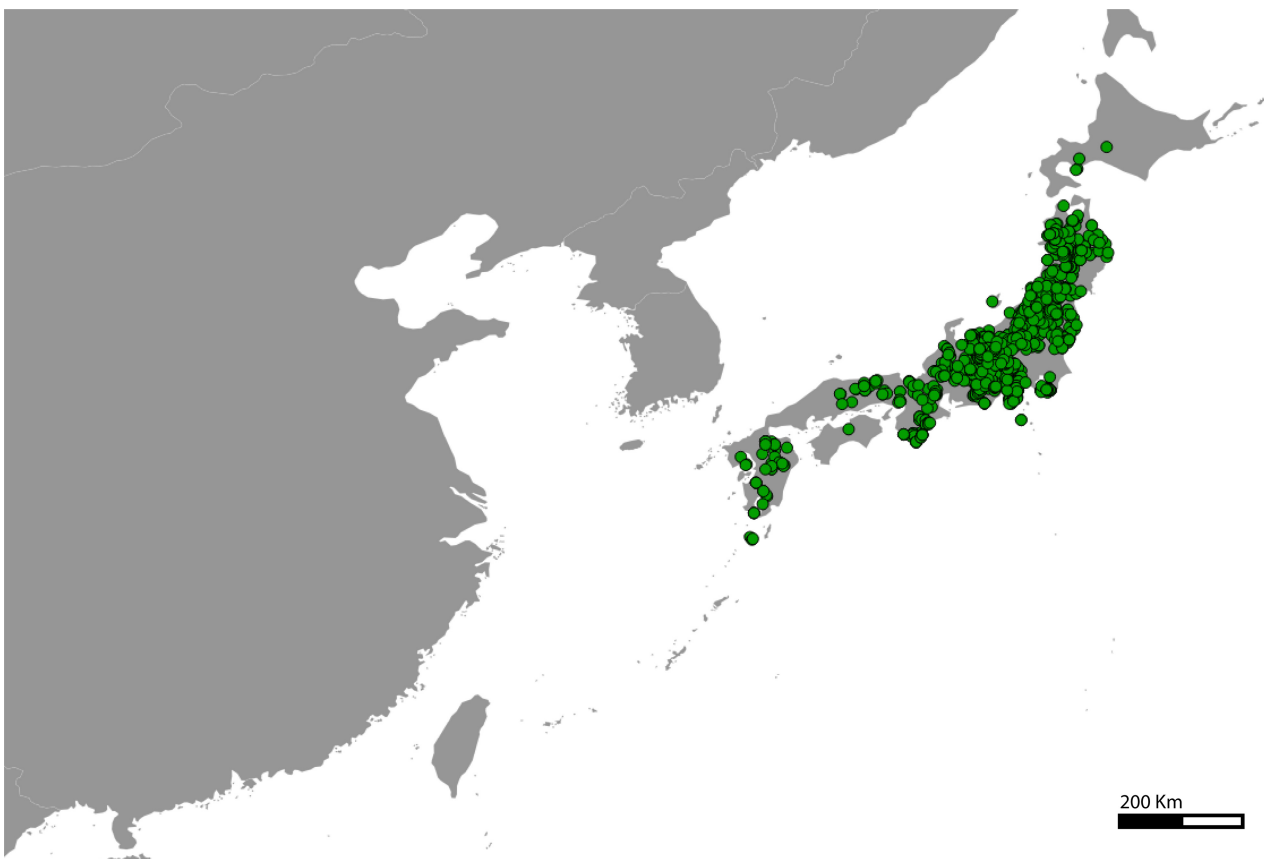


FIGURE 6. Distribution of *Spicantopsis amabilis* extracted from GBIF.

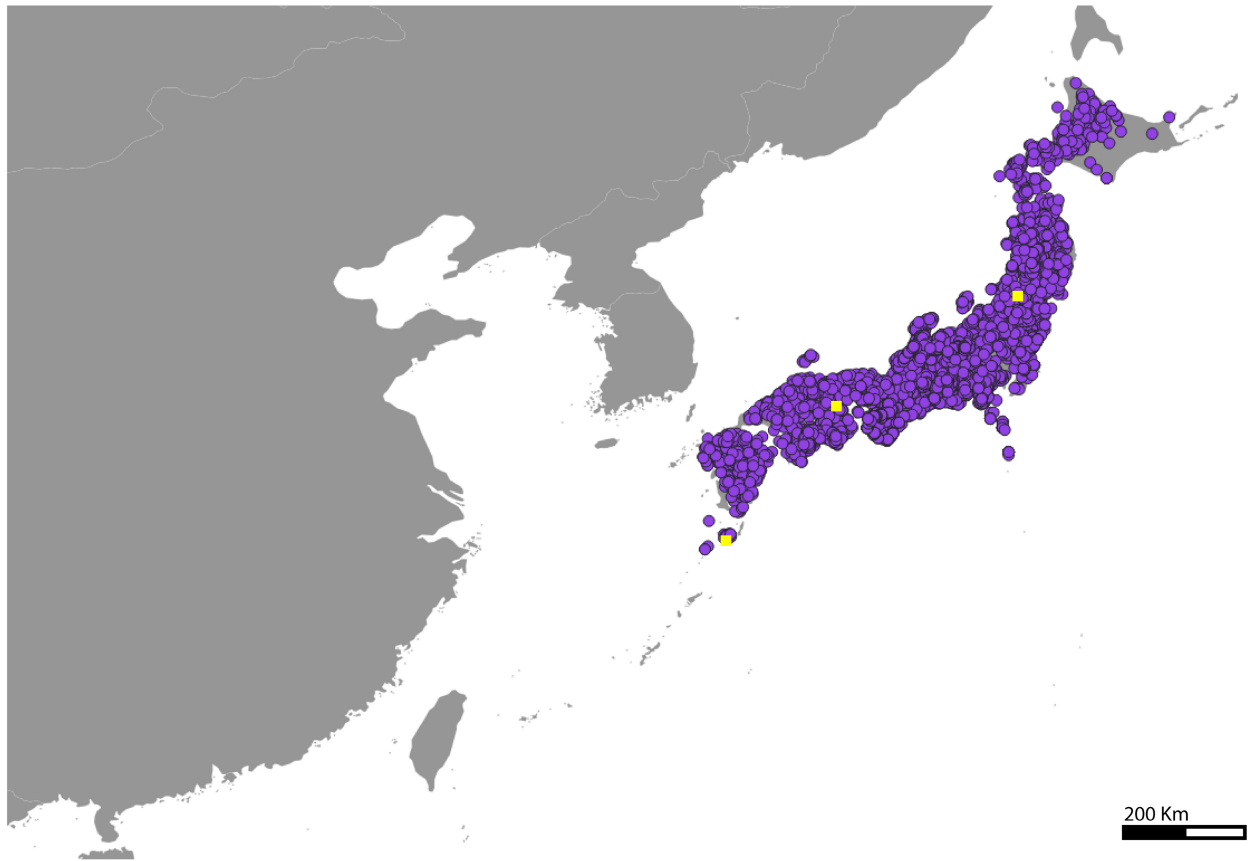


FIGURE 7. Distribution of *Spicantopsis niponica* extracted from GBIF. Purple circles: *S. niponica* var. *niponica*; yellow squares: *S. niponica* var. *minima* (added manually).

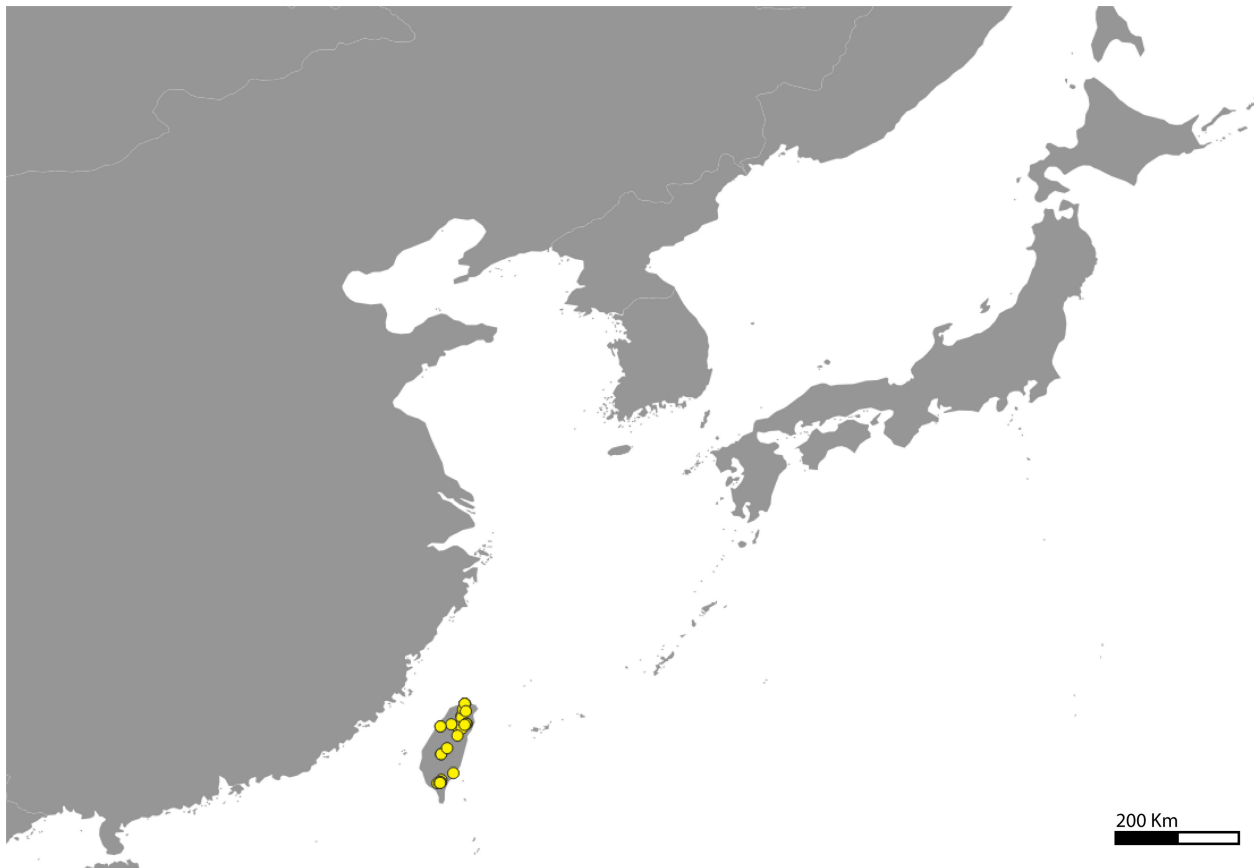


FIGURE 8. Distribution of *Spicantopsis hancockii* extracted from GBIF.

Maps

The mapping was carried out using QGIS 3.12 software (QGIS Development Team 2023). The data used to visualize both the distribution of both genera and the distribution of the different species within each genus were obtained from the Global Biodiversity Information Facility database (GBIF 2023a, b). To ensure the representativeness and quality of the data, specific selections were made from herbarium records. We chose to include only those entries in the database that originated from material deposited in different herbaria. A total of 176,551 records were obtained for the genus *Struthiopteris*, and 8,806 records for the genus *Spicantopsis*.

TAXONOMIC TREATMENT

Spicantopsis Nakai (Figure 9A–C; Figure 10).

Type:—*Spicantopsis niponica* (Kunze) Nakai.

Plants terrestrial; *rhizomes* either creeping and slender or erect and thick, not stoloniferous, dark, covered with scales; *scales* concolorous or discoloured, light brown to dark brown, linear-lanceolate or ovate-lanceolate, membranaceous or papyraceous, with entire margins; *fronds* forming a rosette, dimorphic, *sterile fronds* with *stipes* slender, short, light brown or green, proximally covered with scales, *laminae* lanceolate, erect or arcuate, pinnate to pinnatisect to pinnate, apices conform to subconform, glabrous or with small triangular-lanceolate scales, *pinnae* adnate, oblong-linear to linear-falcate, with entire margins, reduced towards the base; *veins* free, simple or 1-furcate, catadromous, ending in very patent adaxial submarginal hydathodes, with a series of parallel intramarginal stomata not following secondary veins; *fertile fronds* erect and pinnate, *pinnae* contracted, *rachis* proximally with small filiform scales or glabrous (*S. amabilis*); *sori* linear and continuous, forming coenosori on both sides of the costa, occupying the entire length of the pinna, not decurrent towards the rachis; *indusia* linear, continuous, long and coiled, open towards the costa; *sporangia* with 19–29 arc cells; *spores* monolete, perispore brown, irregularly reticulate or verrucose granular.

Distribution:—Japan and Taiwan (Figure 5).

Basic chromosome number:— $2n = 31$.

Taxonomic notes:—The genus to which *Spicantopsis* is most closely related is *Struthiopteris*, and in fact has been considered part of it until recently (Gasper *et al.* 2016, 2017, PPGI 2016), subsequently being resurrected (Molino *et al.* 2019b). *Spicantopsis* has pale-brown stipes, sori with straight bases, glabrous epidermis, and stomata that do not follow a pattern following the veins, the latter character being the one that was used to propose its separation from *Struthiopteris* the first time (Nakai 1933). On the other hand, *Struthiopteris* has dark brown to atropurpureous stipes, decurrent sori, epidermis with red glandular hairs on the abaxial side, and stomata located following the veins. They can also be distinguished by the spores, which have a compact perispore in *Spicantopsis* (Figure 9A–C) and are alveolate in *Struthiopteris* (Figure 9D–H). The other two genera to which it is phylogenetically most closely related are *Brainea* Smith (1856: 5) and *Blechnidium* Moore (1860: 210) (Gasper *et al.* 2016, 2017, Molino *et al.* 2019b). However, morphologically they are not similar, these genera being monomorphic or subdimorphic plants with anastomosing venation (vs. dimorphic plants with free veins in *Spicantopsis*). Despite not being phylogenetically closely related, it has some resemblance to some species of the genus *Austroblechnum* Gasper & V.A.O. Dittrich in Gasper *et al.* (2016: 202), but differs in the margins of the pinnae, which are crenulate to serrate in *Austroblechnum* and entire in *Spicantopsis*, however, the diagnostic value of this character is subtle as this difference is not always clear. They also differ in the spores, since in *Austroblechnum* the perispore is smooth and never has folds, while in *Spicantopsis* the perispore is reticulate or verrucose (Moran *et al.* 2018, Molino *et al.*, 2020). In addition, *Austroblechnum* has an austral distribution (Gasper *et al.* 2016), while *Spicantopsis* is found only in Japan and Taiwan. Also in a different clade at the phylogenetic level, it is very similar to *Cleistoblechnum* Gasper & Salino in Gasper *et al.* (2016a: 207). It differs in that the fronds of this genus are monomorphic or subdimorphic, the margins of the pinnae are strongly revolute (vs. straight in *Spicantopsis*) and the laminae are more leathery.

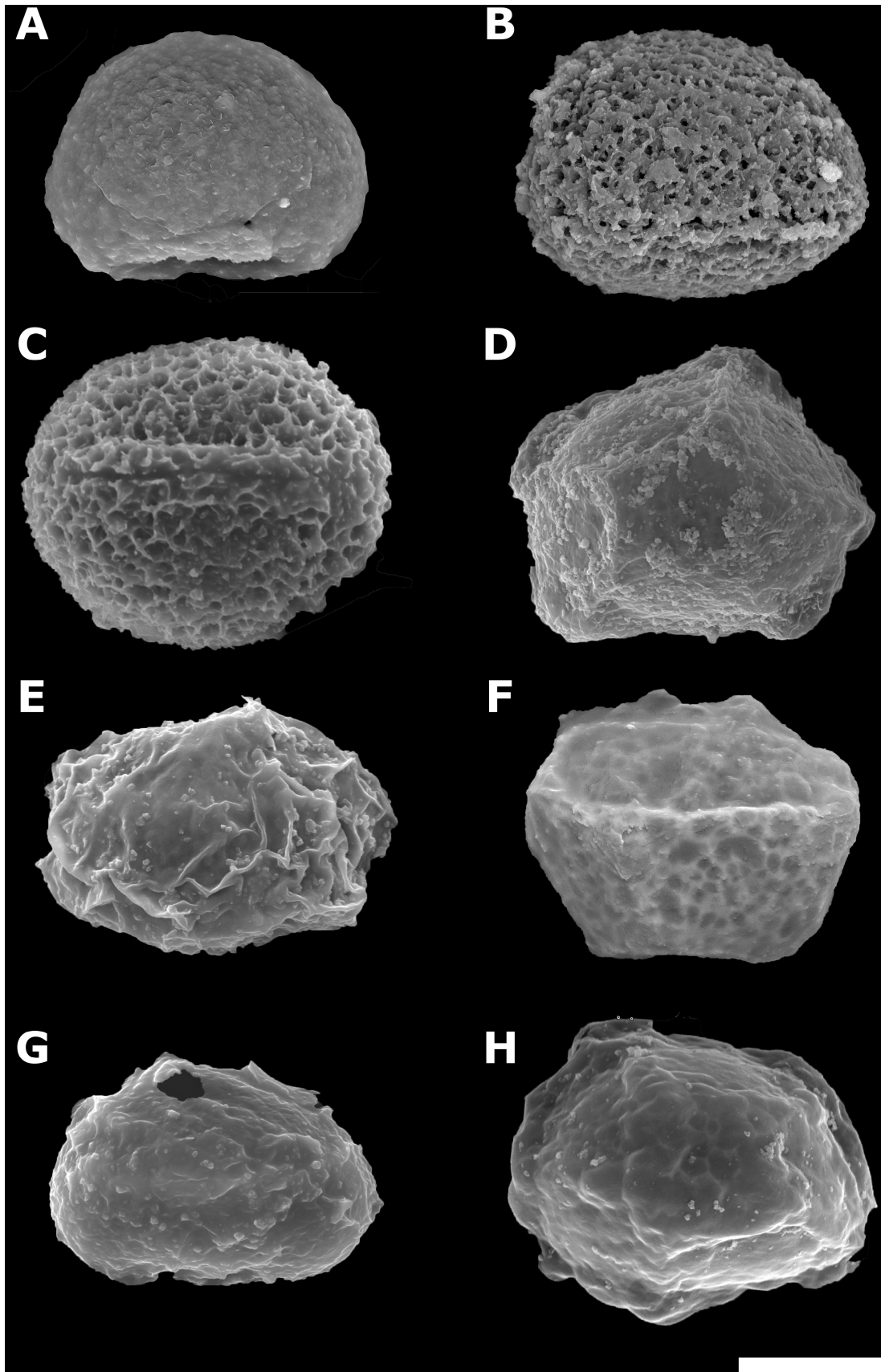


FIGURE 9. Spores of *Spicantopsis*: A. *S. amabilis* (*J. Faurié*, 5612 P01406648). B. *S. hancockii* (*R. Knapp* 4311, P02435597). C. *S. niponica* var. *niponica* (*M. Tagawa & K. Iwatsuki* 3014, P01575937). Spores of *Struthiopteris*: D. *S. castanea* (*Y. Saito s.n.*, TNS792168). E. *S. fallax* (*P. Wasowicz & J.M. Gabriel y Galán s.n.*, MACB 109359); F. *S. spicant* var. *spicant* (*A. Santos s.n.*, MACB36152). G. *S. spicant* var. *homophyllum* (*Barrera s.n.*, MACB32367); H. *S. spicant* var. *pradae* (*S. Molino et al s.n.*, MACB110654). Bar = 30 μm in A–D; 22 μm in E–H.

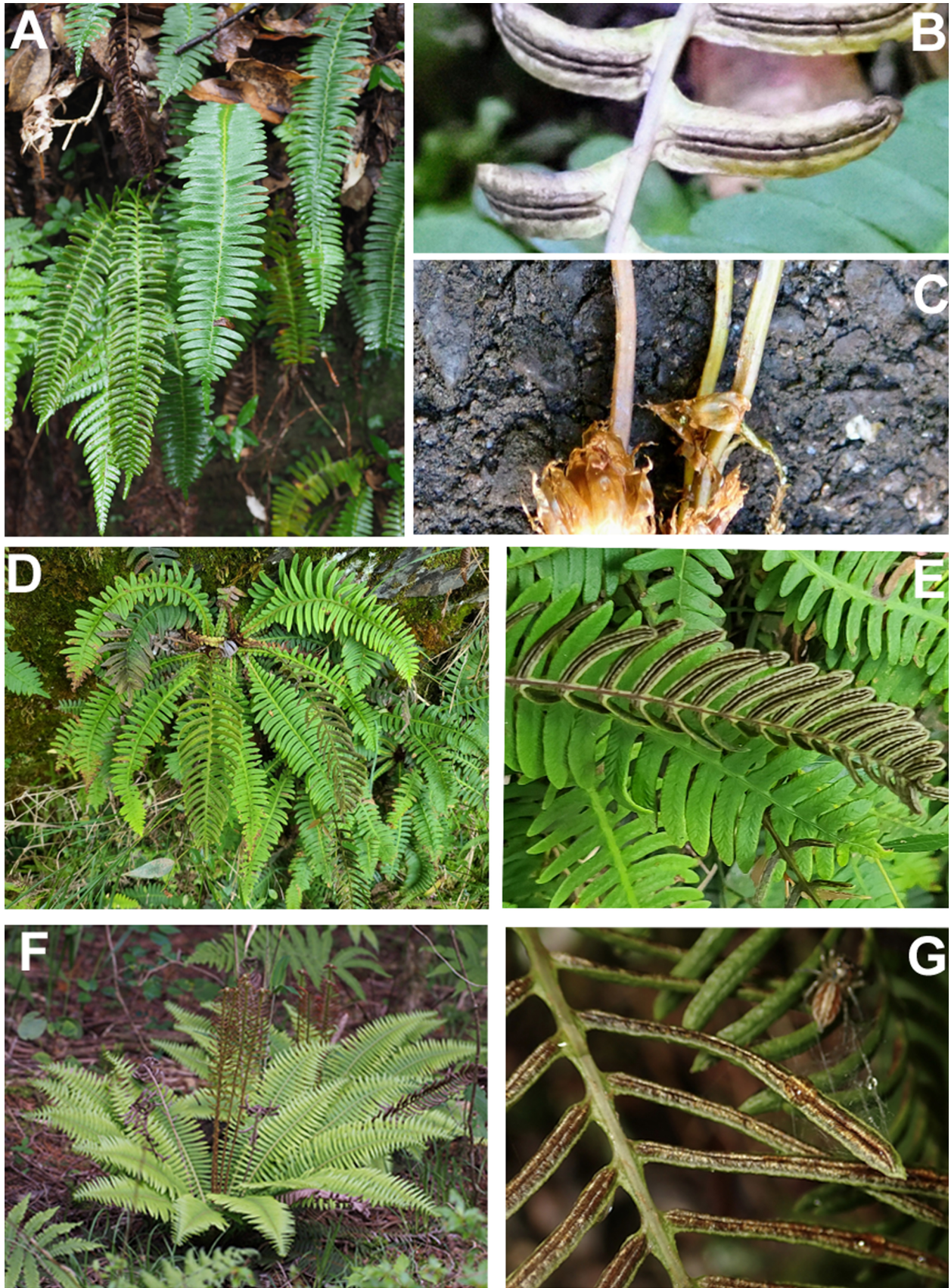


FIGURE 10. *Spicantopsis* species in the field. A–C. *Spicantopsis amabilis*. A. Habit; B. Detail of the abaxial side of the fertile pinnae, bearing sori; C. Detail of the rhizome scales; D–E. *Spicantopsis hancockii*. D. Habit; E. Detail of the abaxial side of the fertile frond, bearing sori; F–G. *Spicantopsis niponica* var. *niponica*. F. Habit; G. Detail of the abaxial side of the fertile frond, bearing sori. Pictures: A. Kimitsu, Chiba, Japan, by Keita Watanabe; B & C. Hichiso, Gifu, Japan, Yukihiro Emoto; D & E. Yilan, Taiwan, by Gu Jianye; F. Fujinomiya, Shizuoka, Japan by Harum Koh; G. Izumi, Osaka, Japan, by Tatsuya Fujiwara.

Identification key to *Spicantopsis* species.

1. Rhizomes short and erect with long, linear-lanceolate, papyraceous, discoloured scales, with sclerotized centre; laminae with small triangular-lanceolate scales; costae adaxially grooved 2.
- Rhizomes short creeping with ovate, membranaceous, concolorous scales, without sclerotized centre; laminae glabrous, costae not adaxially grooved *S. amabilis*
2. Sporophylls distinctly longer than trophophylls. Sporangia with two posterior cells.....3
- Sporophylls shorter or about the same size as trophophylls. Sporangia without two posterior cells *S. hancockii*
3. Plants taller than 15 cm at maturity *S. niponica* var. *niponica*
- Plants no longer than 15 cm at maturity *S. niponica* var. *minima*

Spicantopsis amabilis (Makino) Nakai (Figure 9A; Figure 10A–C; Figure 11).

Type:—JAPAN. Awa Prov., Mt. Kiyosumi, 6 April 1896, *T. Makino s.n.* (MAK113467! photo, lectotype, **designated here**; MAK115262! photo, isolectotype).; JAPAN. Musashi Prov., Chichibu, Mt. Yokami, 16 July 1888, *T. Makino s.n.* (MAK113468! photo, MAK115263! photo, syntypes); JAPAN. Sabami Prov., Hakone-tonosawa, 31 December 1893, *M. Matsuda s.n.* (MAK113469! photo, syntypes).

Synonyms:—*Blechnum amabile* Makino. *Spicanta amabilis* (Makino) Nakai (1928: 12). *Struthiopteris amabilis* (Makino) Ching (1940: 243). *Lomaria amabilis* (Makino) Ching (1940: 5).

Invalid designations: *Lomaria crenulata* Moore in Hooker & Baker (1867: 180) nom. nud.; *Blechnum crenulatum* Salomon (1883: 115).

Plants terrestrial; *rhizomes* short to more or less long creeping, covered with concolorous, light brown, ovate-lanceolate, membranaceous scales, 1–2 (4) x 2–7 (11) mm, apices acute, margins entire, slightly cucullate; *fronds* dimorphic; *sterile fronds* (10) 21 (35) cm long, *stipes* brown or green (0.5) 2 (10) cm long, *laminae* linear-lanceolate, coriaceous, (1.5) 3 (5) x 10–17 (30) cm, 1-pinnate or pinnatisect, apex conform, glabrous, *rachis* brown or green, without adaxial groove, glabrous, *pinnae* tapering towards base, the middle ones 0.2–0.5 x 0.8–2.5 cm, *costae* brown or green, glabrous; *veins* simple or 1-furcate, free, catadromous, ending in submarginal patent hydathodes; *fertile fronds* about the same length as sterile ones, sometimes shorter, *stipes* short, green, (1) 3–13 cm, *laminae* lanceolate, narrower than the sterile ones (1.5–3 cm wide), 1-pinnate, apex conform, *rachises* brown or green, glabrous, without adaxial groove, *pinnae* contracted, the middle ones 0.15–0.5 x 0.6–2 cm; *sori* linear, continuous, forming coenosori on both sides of costa, covering entire length of pinna, not decurrent to rachis; *indusia* linear, continuous, open to costa, long and coiled; *sporangia* with 20–26 arc cells; *spores* monoete, 30–50 x 50–70 µm, brown, with verrucose-granular perisporium.

Habitat and distribution:—Endemic to Japan, in Honshu, Shikoku (Kochi prefecture) and Kyushu (Figure 6). Grows on rock outcrops in the undergrowth of the mountainous zone, and on rocky slopes and cliffs (Ohwi 1953, Iwatsuki 1992, Iwatsuki *et al.* 1995). 300–1700 m.

Chromosome number:— $2n = 62$, diploid (Fabbri 1965, Kurita 1965, Nakato 1987).

Etymology:—Makino applied the Latin epithet *amabile* (amiable, pleasant) to this taxon apparently due to its slender and graceful habit. The vernacular, *osashida*, means “loom-comb fern”, probably because of its resemblance of its fronds to this object.

Vernacular names:—*Osashida* (オサシダ, Japanese) (Iwatsuki 1992).

Taxonomic notes:—It differs from the other species of the genus in its rhizome scales, which are membranaceous, concolorous and ovate-lanceolate, whereas *S. hancockii* and *S. niponica* show papyraceous, linear, discoloured, sclerotized scales. Spores have a verrucose-granular perispore in *S. amabilis*, which is irregularly reticulate in the other species.

In the protologue, Makino cites several syntypes (Makino 1897). We have selected *T. Makino s.n.* (MAK113467) as lectotype (since it is the one in which the long creeping rhizome, the character Makino considered most distinctive, is most evident) and *T. Makino s.n.* (MAK115262) as isolectotype.

During our revision we found an undated and apparently old specimen allegedly collected in China (Sichuan) that lies within the morphological circumscription of *S. amabilis* (*E. Faber 1028*, NY!). However, we prefer to consider this presence doubtful given the scarce information available (there is no information about county, province, or city) until it can be verified with more precise records.

Additional specimens examined:—JAPAN. Honshu: **Pref. Aomori:** Aomori-shi, 18 October 1981, *M. Neichi s.n.* (TNS517591! photo); Imabetsu-machi, 23 October 1977, *N. Saitoh* (TNS517423! photo); Noheji-machi, 18 August 1972, *T. Sudo s.n.* (TNS517425! photo); *ibidem*, 31 August 31, *T. Sudo s.n.* (TNS517674! photo); Oirase, 4 August 1977, *T. Naito s.n.* (MO2697240!); Soma-mura, 28 July 1979, *M. Saito & A. Takahashi s.n.* (TNS517424! photo); Towadako-machi, 31 August 1975, *T. Sudo & M. Sudo s.n.* (TNS463340! photo); *ibidem*, 13 October 1981, *M.*

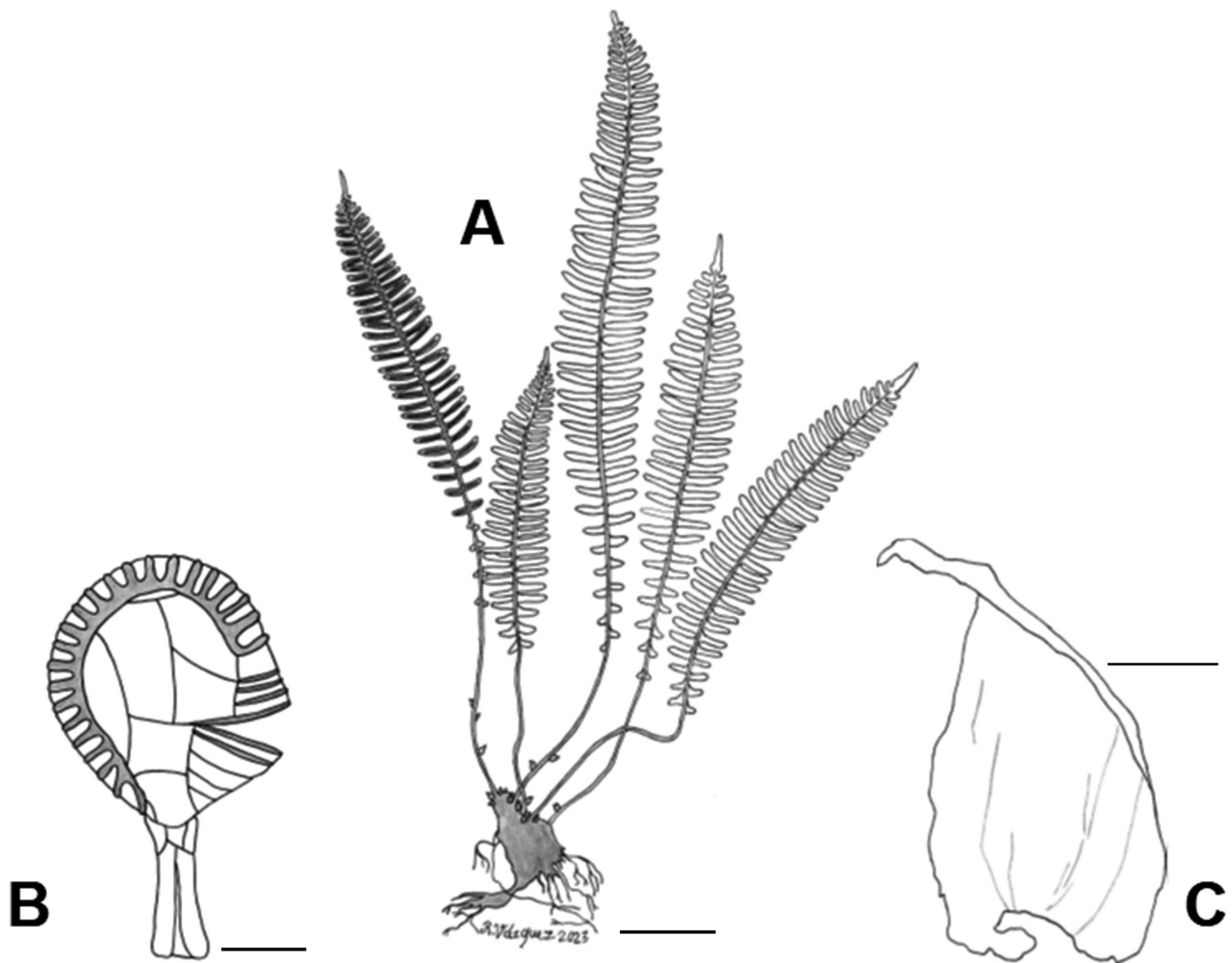


FIGURE 11. Illustration of *Spicantopsis amabilis*. A. Habit (*Nakamura s.n.*, TNS01019335); B. Sporangium (*J. Faurié 5612*, P01406648); C. Rhizome scale (*J. Faurié s.n.*, S1953). Scale: 4 cm in A; 100 μ m in B; 1 mm in C.

Neichi s.n. (TNS517426! photo); **Pref. Chiba:** Kazusa-machi, 1 December 1963, *F. Konta 3972* (TNS924822! photo); Mitsuishiyama, Kameyama, Kazusa-cho, Kimitsu-gun, 2 July 1966, *G. Murata & K. Iwatsuki 580* (US2424195!); Mt. Nokogiri, 21 March 1924, *Y. Yamamoto s.n.* (TAIF125401! photo); **Pref. Fukushima:** Yama-gun, Kitashiobara-mura, Nakatsugawa Gorge, 9 July 1999, *M. Maki et al 997975* (MO5333264!); **Pref. Gifu:** Takayama, 1915, *J. Faurié 51* (NY04179844!); **Pref. Gunma:** Kusatsu, 1877, *M. Dickins s.n.* (P01406525!); Hyogo, Kobe city, Mt. Rokko, 20 July 1932, *K. Uno 9171* (TAIF461138! photo); **Pref. Iwate:** Kayusa, Mt. Mitsuishi, 13 December 1953, *T. Namegata 3819* (US2138756!); **Pref. Kanagawa:** Kamkura, 1915, *T. Makino 32949* (US2421838!); **Pref. Kyoto:** Oohuse, north of Kyoto, 23 September 1951, *M. Tagawa 4240* (US2258980!); Tadasu-no-mori, 10 July 1888, *J. Faurié 614* (P01567610!); **Pref. Mie:** Miyama.cho, 25 June 1983, *J. Haginiwa* (TNS984311! photo); Utobi, 23 November 1956, *K. Seto 6672* (P01608624!; C0364698F!; US2420040!); **Pref. Nagano:** Kawakami-mura, 6 August 1970, *M. Kato 39* (TNS924821! photo); Shinano, no date, *A. Noguchi s.n.* (MO3155632!); Togakushi, 20 August 1906, *M. Weigel s.n.* (P01571952!); *Ibidem* (P01406644!); Tokiwa, Omachi-shi, Tokiwa, 26 June 1982, *T. Yoshizawa 71566* (TAIF052352! photo); **Pref. Nara:** en route from Mt. Wasamata to Mt. Daifugen, Kamikitayama-mura, Yoshino-gun, 21 September 1986, *S. Tsugaru et al 7438* (MO4012486!); Mt. Shofuken-dake in the Oomine Mountains, 4 August 1962, *M. Tagawa 537* (US2423751!); Shōfuken-dake, 4 August 1962, *M. Tawaga & K. Iwatsuki 5129* (P01575933!); **Pref. Niigata:** Echigo, Takidani, 24 August 1903, *M. Weigel s.n.* (P01406649!); Echigo, Tsugawa, 16 September 1957, *M. Togashi 1576* (MO1734177!; NY04179843!; P01406637!; S1952!; US2259174!); Itoigawa, 3 August 2009, *S. Matsumoto s.n.* (TNS9544305!); Kitauonuma-gun, Irihirose-mura, Ooshirakawa, 22 August 1964, *H. Kanai et al. 8966* (TI00274373! photo); Shibata-shi, 1 July 1962, *F. Konta 402* (TNS924818! photo); *Ibidem*, *F. Konta 981* (TNS924824! photo); *Ibidem*, 27 October 1963, *F. Konta 3394* (TNS924823! photo); *Ibidem*, 27 August 1966, *F. Konta 5698* (TNS924809! photo); *Ibidem*, 1 November 1967, *F. Konta 6741* (TNS924812! photo); **Pref. Saitama:**

Chichibu-gun, Ohtaki-mura, 9 July 2002, *T. Iwata s.n.* (TNS1147001!); *Ibidem* (TNS01147002!); Musasi, Ryôgami, 16 September 1957, *M. Tagawa 341* (P01406650!); **Pref. Shiga:** Umenoki to Kawai, Katsuragawa-mura, Shiga-gun, 22 August 1962, *M. Tagawa 8687* (US2551253!); **Pref. Shizuoka:** Amagi-yugashima-cho, 23 July 1966, *F. Konta & M. Wakabayashi 65* (TNS924811! photo; TNS924808! photo); Fuji-shi, 15 September 1983, *T. Sato 4368* (TNS924830! photo); Fujinomiya-shi, 16 September 1984 (TNS924816! photo); Hamamatsu-shi, 8 August 2000, *T. Nakamura s.n.* (TNS1019335!); Misakubo-cho, 10 October 1986, *F. Konta 15891* (TNS924829! photo); Nyuhjima, Umegashima, Sugura, 9 August 1979, *Y. Saiki 1049* (C2103458F!); Shizuoka-shi, 8 August 1973, *F. Konta 10064* (TNS924810! photo); Umegashima-mura, July 1964, *S. Choshi s.n.* (TNS924813! photo); **Pref. Tochigi:** 13 September 1958, *M. Tagawa & K. Iwatsuki 1913* (P01608623!); *ibidem* (US2358631!); **Pref. Tomaya:** Tateyama, August 1913, *J. Faurié 51* (S1953!); *ibidem* (P01406643!); *ibidem* (P01406645!); *ibidem* (P01406646!); **Pref. Wakayama:** Oto-mura, 11 August 1965, *G. Murata & F. Konta 122* (TNS924814! photo); Kii, Owase-machi, Kita-muro-gun, 9 October 1956, *M. Furuse s.n.* (S1951!); Kii, Yukawa, 25 July 1883, *J. Matsumura s.n.* (TI00274283! photo); **Pref. Yamagata:** en route from Higashiootori-dam to Awataki-dam, Asahi-mura, Higashitagawa-gun, 18 July 1990, *S. Tsugaru 13489* (MO4296957!); **Pref. Yamanashi:** Fusiyama, 1864, *Tschonoski s.n.* (P01406532!). **Kyushu: Pref. Kagoshima:** Ibusuki-shi, 28 August 1983, *T. Yamanaka s.n.* (TNS779978! photo); Okuchi-shi, 12 January 1969, *T. Yamanaka s.n.* (TNS734286! photo); Satsuma, July 1888, *J. Faurié s.n.* (P01567609!); Yakushima Island, Yaku-cho, 12 October 2006, *A. Ebihara & M. Ito TF297* (TNS763339!). **Shikoku. Pref. Kochi:** Tosa, Mt. Kaminomine, 13 April 1930, *H. Itô s.n.* (TI00274351! photo). **Unknown location:** no date, *no collector* (P01406642!); 20 August 1910, *no collector* (US1095353!); 9 February 1910, *Christ 94* (P01406586!); August 1913, *J. Faurié s.n.* (P01575934!); 28 August 1898, *J. Faurié 1566* (P01406590!); July 1904, *J. Faurié 5612* (P01406647!); *ibidem* (P01406648!).

Spicantopsis hancockii (Hance) Masam. (Figure 9B; Figure 10 D–E; Figure 12).

Type:—TAIWAN. In rupibus apertis montis olim ignivomi nunc exincti Huangkong, juxta Tam-sui, insulae Formosae, alt. 3300 ped. rarissimum, nec alibi, coll. 27 November 1881, *W. Hancock 87* (Herb. propr. n. 22183, BM001045995! photo, holotype).

Synonyms:—*Blechnum hancockii* Hance; *Lomaria hancockii* (Hance) Baker (1891: 220); *Spicantopsis niponica* (Kunze) Nakai var. *hancockii* (Hance) Nakai (1933: 183); *Struthiopteris hancockii* (Hance) Tagawa (1952: 192).

=*Lomaria apodophylla* Baker (1885: 104). **Type:**—NORTH FORMOSA [TAIWAN]. no date, *W. Hancock 87* (US00065538!, holotype; LE01009883! photo, isotype).

Plants terrestrial, sometimes saxicolous; *rhizomes* erect short, covered with linear-lanceolate, discoloured scales, with the centre broadly sclerotized from base to apex, chestnut or dark red, margins light brown, 0.5–1 x (5) 10 (16) mm; *fronds* dimorphic; *sterile fronds* (11) 27 (45) cm long, shortly petiolate, *stipes* light brown or green, 0.5–1 (4) cm long, *laminae* linear to elliptic-lanceolate, coriaceous, 3–6 (10) x 10–30 (45) cm, 1-pinnate, pinnatifid or pinnatisect, apex subconform, abaxial side with small, concolorous, light brown, triangular-lanceolate scales, *rachises* light brown or green, grooved adaxially, abaxially with scales similar to those on the lamina, *pinnae* tapering towards the base, the middle ones 0.3–0.6 x 1.5–4 (8) cm, tapering towards base, *veins* free, simple or 1-furcate, catadromous, ending in submarginal patent hydathodes; *fertile fronds* shorter or about the same size as sterile ones, *stipes* brownish or green, 1–3 (7) cm, *laminae* coriaceous, 2–5 (8) x 10–30 (48) cm, 1-pinnate, with scales like those on the sterile lamina and rachis, *pinnae* more contracted, the middle ones 0.2–0.4 (0.6) x 1.5–3 (5) cm, tapering toward base; *sori* linear, continuous, forming coenosori on both sides of costa, occupying entire length of pinna, not decurrent towards rachis; *indusia* brown, continuous, long and coiled; *sporangia* with 20–29 arc cells; *spores* monolete, 25–40 x 40–60 µm, perisporium with granular reticulate surface.

Habitat and distribution:—Taiwan (Figure 8). Relatively dry or moist areas, usually on rocky shaded slopes, terrestrial, sometimes saxicolous. 800–2900 m (Iwatsuki 1992, Chiou *et al.* 1994, Iwatsuki *et al.* 1995, Kuo 2001, Ebihara *et al.* 2023).

Chromosome number:— $2n = 62$, diploid (Fabbri 1965, Nakato 1987). There is another chromosome counting on a recent work (Nakato *et al.* 2020), but the specimen is from Japan, where it has been proven that the species does not occur (Ebihara *et al.* 2023), so it is probably a specimen of *S. niponica*.

Etymology:—The taxon honors William Hancock (1847–1914), Irish botanist and collector of the type specimen during his tenure as customs officer in China and Taiwan (Bionomia 2023).

Vernacular names:—Kuān yè jiá náng jué (宽叶荚囊蕨, Chinese); Haku-un-shida (ハクウンシダ, Japanese) (Iwatsuki 1992, Faguo *et al.* 2013). The Japanese name, haku-un-shida, means “fern of the white cloud”, we have no certainty of the reason of this name. The Chinese name, Kuān yè jiá náng jué, means “pod fern”, we are not certain why either.

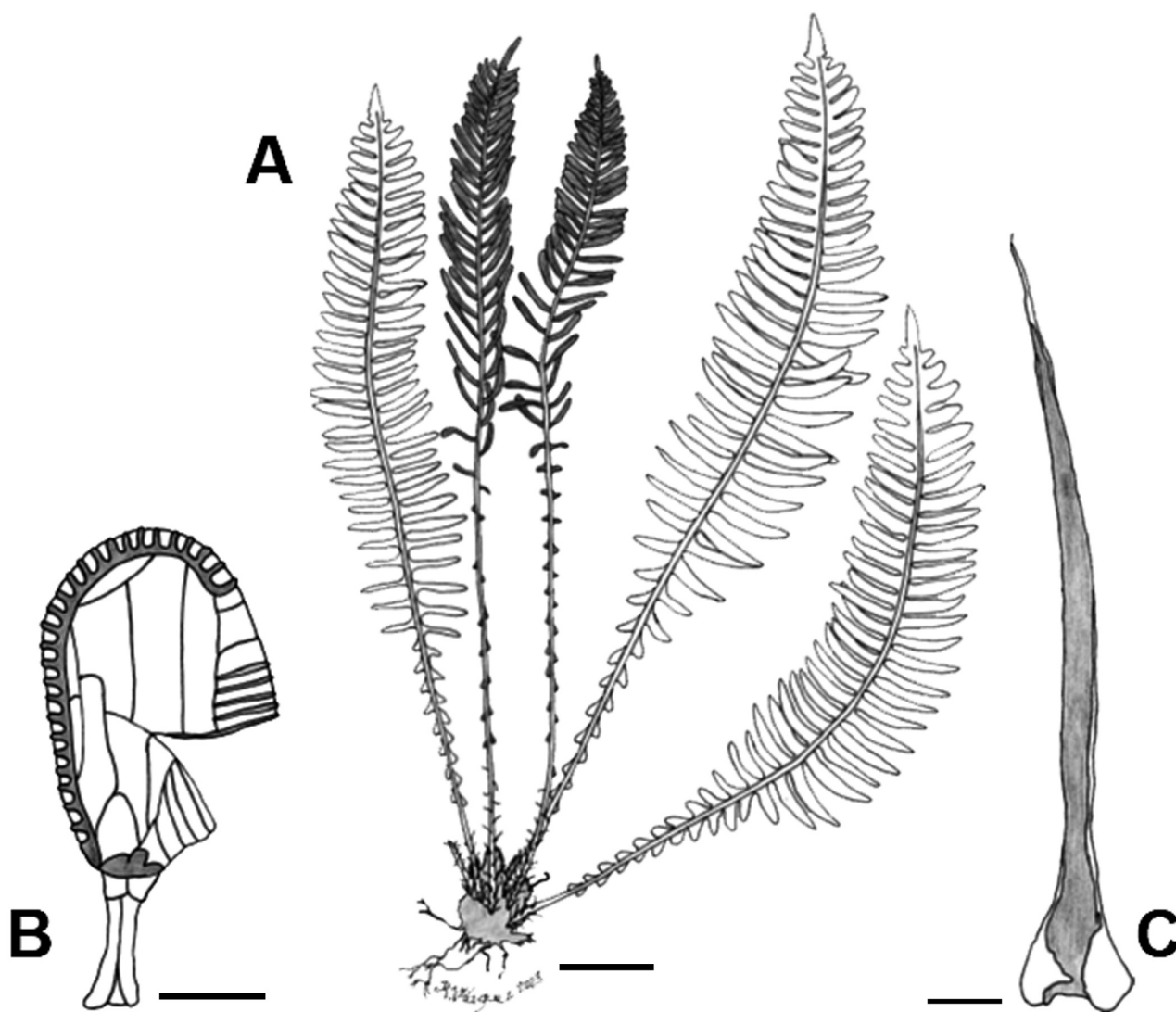


FIGURE 12. Illustration of *Spicantopsis hancockii*. A. Habit (Y.-H. Chang 60, TAI278160); B. Sporangium (R. Knapp 3338, P02439073); C. Rhizome scale (R. Knapp 3430, P02439164). Scale: 4 cm in A; 100 µm in B; 500 µm in C.

Taxonomic notes:—*Spicantopsis hancockii* is very similar to *S. niponica*, and in fact, authors such as Nakai (1933) or DeVol (1975) considered they could be the same species or, at most, varieties of the same species. However, recent studies consider them as two distinct species (Itwasuki *et al.* 1995, TPG 2019, Molino *et al.* 2019b, Ebihara *et al.* 2023). Different distinguishing characters have been proposed, for example Otaga (1941) and Nakaike (1982) noted differences in the fertile fronds (shorter than sterile in *S. hancockii* and conversely in *S. niponica*), pinna margins (recurved in *S. hancockii*), pinna scales (with “marginal hairs” in *S. hancockii* and without them in *S. niponica*) and spore size (larger in *S. hancockii*). Ebihara (2016), however, did not find the differences in scales, while he observed marginal excretions in both species, an aspect also seen by us. Molino *et al.* (2020) found the opposite relationship in the spores (those of *S. niponica* being slightly larger), and noticed that the sporangia were clearly differentiable, with two posterior cells in the case of *S. niponica* and no posterior cells at all in the case of *S. hancockii*. Relative length of sporophylls relative to trophophylls (sporophylls shorter than trophophylls in *S. hancockii* and the reverse in *S. niponica*) has proven useful, however it may be confusing in some immature specimens of *S. niponica*, with shorter sporophylls (Ebihara *et al.* 2023). In these cases, the examination of the sporangium seems the only reliable character (Molino *et al.* 2020, Ebihara *et al.* 2023). It is also similar to its congener *S. amabilis*, but the size of the plant and differences in the rhizome scales easily separate them (see *S. amabilis* section). In addition, it has been shown that *Spicantopsis hancockii* does not coincide in distribution with *S. amabilis* and *S. niponica*, the former growing only in Taiwan and the other two only in Japan (Ebihara *et al.* 2023). It can be confused with *Cleistoblechnum eburneum* (Christ) Gasper & Salino, with which it coincides in distribution. They can be differentiated because *C. eburneum* has

fronds with very slight dimorphism, the margins of the pinnae are strongly revolute and the laminae are coriaceous, whereas in *S. hancockii* the fronds are strongly dimorphic, the margins of the pinnae are straight, and the laminae are less leathery than in *C. eburneum*.

Several authors have considered that *S. hancockii* is present in the Tokara Islands, Japan, based on different collections (Hatsushima 1962, Hatusima 1986, Sako 1978, Shiuchi & Hotta 2015, Suzuki *et al.* 2022). On the other hand, other authors considered that these collections are indeed *S. niponica* (DeVol 1975, Kurata & Nakaike 1987, Chiou *et al.* 1994, Kuo 1997, 2001, Ebihara 2016). Recently, Ebihara *et al.* (2023) have confirmed by molecular techniques and micromorphology that specimens from the Tokara Islands are indeed *S. niponica*, confirming that *S. hancockii* is a strict Taiwanese endemic.

Additional specimens examined:—TAIWAN. Chiayi: Alishan, 25 December 1928, *Y. Kudo & S. Suzuki s.n.* (NL996085! photo); *Ibidem*, 2–4 April 1973, *C.M. Kuo 3099* (TAI161616! photo; TAI271480! photo); *Ibidem*, 2–4 April 1973, *C.M. Kuo 3121* (TAI161754! photo); *Ibidem*, 2 January 1994, *S.-J. Moore 16657* (TAIF486372! photo; TAIF486373! photo); *Ibidem*, 1 March 2008, *P.-F. Lu 15930* (TAIF303877! photo); *Ibidem*, 2 July 2014, *Tashan et al. s.n.* (TNS1219667!); Alishan, Arisan, 22 July 1970, *T. Iwasaki s.n.* (TNS832514!); Alishan, Mienyueh, *T.-C. Hsu 9408*, 13 July 2017 (TAIF509453! photo); Alishan, Mt. Ta, 1 March 2008, *C.-W. Chen Wade564* (TAIF389749! photo); Alishan, Zhaoping, Mt. Ta, 2 July 2014, *Y.-H. Chang 20140702-011* (TAIF453698! photo); Mt. A-li, 25 October 1962, *M.T. Kao & C.S. Feung 153* (TAI004260! photo). **Hsinchu:** Jianshih, Meiyuan, Jianshih, Mt. Niaotsui, 12 July 2009, *P.-F. Lu 18523* (TAIF335193! photo); Jianshih, Mt. Litung, 6 September 2009, *C.-W. Chen Wade969* (TAIF397475! photo); Kuan-wu, 99 Hostel to Ta-pa-chien Shan, 4 April 1972, *C.C. Hsu & C.S. Kuoh 13980* (TAI147992! photo); Ta-pa-chien Shan, 10 August 1972, *C.M. Kuo 1756* (TAI153035! photo; TAI159196! photo); *ibidem*, 11 August 1972, *C.S. Kuoh 3321A* (TAI157143! photo). **Hualien:** Erhtzushan, 6 September 1983, *T.-T. Lin & Y.-F. Chen 7153* (TAIF216160! photo); Jeisui logging trail, 16 November 2007, *P.-F. Lu 14917* (TAIF291133! photo); Mt. Muh-kwa, 24 July 1961, *M.T. Kao 4140* (MO3692478!; TAI004256! photo; TAI126342! photo; TAI157281! photo); Muh-Kwa, 24 July 1961, *M.T. Kao 4141* (TAI004259! photo); Taipingchichi, 20 September 1999, *M.-L. Weng 1598* (TAI150756! photo; TAI261730! photo). **Illan:** Datong, Provincial Rd. No. 7A, 27 September 2007, *F.-W. Li FWL560* (TAIF371276! photo); Datong, Ssuyuan-yaku, 18 October 1994, *Y.-H. Chang 60* (TAI278160! photo); *ibidem*, 11 August 2012, *Y.-S. Chao 1965* (TAIF435569! photo); Datong, Taipingshan (Tsubao), 28 March, 1930, *S. Suzuki 3914* (TAI119360! photo); Mt. Taiping, 20 March 1963, *C.S. Feung & M.T. Kao 366* (US2635362!; TAI004261! photo); *ibidem*, 4 March 1966, *C.C. Chuang & M.T. Kao 4136* (TAI004258! photo); *ibidem*, 4 March 1967, *M.T. Kao 6794* (TAI004257! photo); Nan'ao, Mt. Nanhu, 27 September 2007, *E. Schuettpelz et al. 1175B* (TAIF288823! photo); Nan-ao, Mt. Tung, 4 November 2012, *P.-F. Lu 24831* (TAIF403619! photo); Nan'ao, Taipingshan, 7 August 1981, *W.-L. Chiou s.n.* (TAIF166973! photo); *Ibidem*, 28 January 1994, *J.C. Wang et al. 9308* (TAIF79814! photo); *Ibidem*, 3 September 2016, *R. Knapp 4311* (P02435597!); *Ibidem*, 5 December 2005, *R. Knapp & J.-Y. Huang 239* (P02436496!); Nan'ao, Taipingshan, National Forest Recreation Area, Cueifong Lake Circle Trail, 20 June 2008, *A. Ebihara et al. s.n.* (TNS776516!); Nao'ao, Tsuifeng lake, 28 February 2004, *P.-F. Lu 7611* (TAIF202731! photo); Nan-hu-ta-shan, 16 October 1977, *J.-C. Wang 1723* (TAI198587! photo); Nan-shan, April 1944, *unknown collector 417* (TAI161743! photo; TAI161747! photo); Taipingshan, 14 May 1992, *S.F. Huang 4771* (TAI222807! photo). **Kaohsiung:** Chienchin-Kuaishan, Miharasi-Hinokiyama, 9 December 1937, *Yamamoto 615* (TAI004265! photo); Shih-shan, 23 January 1972, *C.M. Kuo 664* (U0043511! photo; TAI161755! photo); *ibidem*, 14 November 1972, *C.M. Kuo 2456* (TAI162439! photo); *ibidem*, *C.M. Kuo 6507* (TAI146786! photo). **Miaoli:** Taian, Leshan logging trail, 27 May 2004, *P.-F. Lu 7940* (TAIF210083! photo). **Nantou:** Dayuling, 14 July 2007, *R. Knapp 1413* (P02437438!); Luantashan, 28 April 1922, *S. Kudo s.n.* (TAIF126083! photo); Sinyi, Chunta logging trail, 27 November 2012, *Y.-H. Chang 20121127-003* (TAIF444888! photo; TAIF444889! photo); *Ibidem*, 9 September 2013, *H.-C. Hung s.n.* (TAIF452653! photo); Sinyi, Kuankao, Tuikuan, 15 December 2011, *T.-C. Hsu 5195* (TAIF387835! photo); Sinyi, Shuanglung logging trail, 12 September 2012, *H.-C. Hung & Y.-H. Chang 20120912-004* (TAIF408677! photo). **Pingtung:** Gaoshu, Dr. Cecilia Koo Botanic Conservation Center, 5 February 2014, *L.-Y. Kuo & C.-M. Chen 3927* (TAIF447324! photo); *Ibidem*, *L.-Y. Kuo & C.-M. Chen 3928* (TAIF447323! photo); Peitawushan, 7 February 1987, *B.-J. Wang 12942* (TAIF162091! photo; TAIF162092! photo); Peitzasuahzn, 27–29 January 1978, *Y.C. Jeng 2744* (TAI277663! photo); Taiwu, Kuaiku, Tawu Shrine, 8 October 2006, *P.-F. Lu 12661* (TAIF184495! photo); Wutai, Hsiaokuei lake, 18 February 2015, *P.-F. Lu 27885* (TAIF460900! photo). **Taichung:** Baxian Mountain [Eight Immortals Mountain], 24 October 1929, *S. Suzuki 2960* (TAI067582! photo; TAI161746! photo); Heping, 710 logging trail, 27 September 2007, *Y.-H. Chang* (TAIF296602! photo); Heping, Mt. Loyehwei, 25 April 2015, *P.-F. Lu 28041* (TAIF465472! photo); *Ibidem*, 1 August 2015, *P.-F. Lu 28511* (TAIF467412! photo); Heping, Ssuyuan-yakou, Mt. Nanhu, 1 July 2009, *Y.-H. Chang 20090701-021* (TAIF400098! photo); Nanhu Dashan, October 1928, *S. Sasaki s.n.* (TAI004270! photo); Mt. Hassenzari, 23 October 1929, *S. Suzuki s.n.* (TAI007530! photo); Pa-Shen-Tun to Mt. sin Shan, 7 August 1959, *T.C. Huang 1321* (TAI004267! photo).

photo); Pa-shien-shan, 5 November 1969, *T.C. Huang 1336* (TAI12776! photo); Pahsinshan, 7 August 1959, *Huang 1321* (TAI004272! photo); Pahsinshan Logging Station, 7 August 1959, *T.I. Chuang et al. 2751* (TAI004262! photo; TAI004264! photo); Ssuyuan, 11 January 2001, *J.-H. Li & C.-K. Liou 399* (TAIF153000! photo; TAIF153001! photo). **Taipei:** Beitou, 18 January 2014, *R. Knapp 3338* (P02439073!); Beitou, Chihsing, 28 February 2003, *P.-F. Lu 5529* (TAIF187192! photo); *Ibidem*, 19 September 2009, *Y.-H. Chang 20090919-004* (TAIF366933! photo); *Ibidem*, 1 June 2013, *P.-F. Lu 25597* (TAIF418892! photo); Chihshingshan, 16 July 1974, *C.E. DeVol 1202* (TAI187939! photo); *ibidem*, 14 June 2000, *P.-H. Lee 300* (TAIF115743! photo); *Ibidem*, 12 January 2002, *P.-F. Lu 2908* (TAIF155311! photo; TAIF155312! photo); Mt. Seven Star, 11 October 1963, *M.T. Kao 5466* (TAI004266! photo); Sitisei, Chihshingshan, 2 September 1926, *S. Suzuki s.n.* (TAI004269! photo); Peichatenshan, 28 September 1984, *R.T. Li 3583* (TAI196166! photo); *ibidem*, *R.T. Li 3584* (TAI196165! photo); *ibidem*, *R.T. Li 3585* (TAI196164! photo); Taiping, 20 February 1963, *Feung & Kao 336* (TAI004261! photo); Tsi-hsin-shan, 15 November 1972, *C.P. Ling 2468* (TAI148816! photo); Tsi-hsin-shan (Suen Star Mt.) 28 January 1924, *no collector s.n.* (TAI132647! photo). **Taitung:** Beinan, Chihpen logging trail, 6 December 2012, *C.-F. Chen 4361* (TAIF423999! photo); Taiwu, 2 June 2014, *R. Knapp 3430* (P02439164!; P02439165!); Yanping, Yenping logging trail, 10 December 2002, *P.-H. Lee 2326* (TAIF182691! photo; TAIF182691! photo). **Taoyuan:** Fushing, en route from Takuanshan Forest Reserve to Tamanshan, 9 April 2002, *W.-C. Leong 2786* (MO6428317!); Fusing, Howi Giants Group, New Taipei City, Sansia, Mt. Peichantien, 7 August 2011, *C.-W. Chen Wade1658* (TAIF397367! photo); Fushing, Mt. Fufu, 19 June 2010, *T.-C. Hsu 2838* (TAIF392212! photo); Fushing, Mt. Peichantien, 1 November 2014, *P.-F. Lu 27372* (TAIF456353! photo); Kaohsiung city, Chyunshan logging trail, 5 February 1992, *B.-J. Wang 18990* (TAIF165847! photo; TAIF165848! photo; TAIF165849! photo; TAIF165850! photo; TAIF165851! photo). **Unknown location:** 1 August 1906, *H. Shakurai s.n.* (P01406577!).

Spicantopsis niponica (Kunze) Nakai (Figure 9C; Figure 10F–G; Figure 13A, D, E).

Type:—JAPAN. Hondo, Suwo, Hikami oppida Ouchi, no date, *J. Nikai 12* (TI00274317! photo, neotype, **designated here**).

Synonyms:—=*Lomaria niponica* Kunze. *Blechnum niponicum* (Kunze) Makino (1897: 82). *Blechnum spicant* (L.) Roth (1794: 56) var. *niponicum* (Kunze) Christensen (1906: 405). *Spicanta niponica* (Kunze) Hayata (1927: 700) (original: ‘*nipponica*’). *Struthiopteris niponica* (Kunze) Nakai (1930: 15) (original: ‘*nipponica*’).

=*Lomaria spicant* (L.) Desvaux (1811: 350) var. *japonica* Hooker (1860: 15) (original: ‘*β. Japonica*’). **Type:**—JAPAN. Hakodadi, 1853–56, *C. Wright s.n.*, North Pacific Exploring Expedition (US bc01527323!, holotype) =*Spicantopsis niponica* (Kunze) Nakai (1933: 181) var. *japonica* (Hook.) Nakai (1933: 181).

=*Blechnum spicant* (L.) Roth var. *reflexipinnula* Masamune (1932: 303). **Type:**—JAPAN. Yakushima, 1928, *Aikodake* (not found, synonymy based on the protologue and current usage of the name). =*Spicantopsis niponica* (Kunze) Nakai var. *reflexipinnula* (Masam.) Nemoto (1936: 75). *Struthiopteris niponica* (Kunze) Nakai var. *reflexipinnula* (Masam.) Masamune (1951: 198).

=*Blechnum spicant* (L.) Roth var. *undulatipinnula* Masamune (1932: 303). **Type:**—JAPAN. Mt. Takakuma, 1922, *no collector* (not found, synonymy based on the protologue and current usage of the name); =*Spicantopsis niponica* (Kunze) Nakai var. *undulatipinnula* (Masam.) Nemoto (1936: 75).

=*Spicantopsis niponica* (Kunze) Nakai f. *flabellata* Satō (1936: 824, Fig. 2). **Type:**—JAPAN. Insula Yakushima, inter Kosugidani et Nakanokoya, 24 August 1935, *K Satō s.n.* (not found, synonymy based on the protologue and current usage of the name). =*Struthiopteris niponica* (Kunze) Nakai (1933: 181) f. *flabellata* (Satō) Namekata & Kurata (1961: 332).

=*Struthiopteris niponica* (Kunze) Nakai f. *kinoshitae* Itō (1971: 38). **Type:**—JAPAN. Shikoku: mamidani, Tazukawa, Katsuura-machi, Katsuura-gun, Tokushima Pref., 10 October 1970, *S. Kinoshita s.n.* (TI00081476! photo, holotype).

Plants terrestrial; *rhizomes* thick, short and erect, covered by linear scales (0.6) 1–2 x (2) 11–16 mm, papyraceous, discoloured, centre broadly sclerotized from base to apex, red or dark brown, margins narrow, light brown, entire; *fronds* dimorphic, *sterile fronds* (15) 33 (51) cm long, short petiolate, *stipes* light brown or green, 0.5–6 cm, *laminae* linear to elliptic-lanceolate, coriaceous, (3) 5–8 (10) x 15–30 (48) cm, 1-pinnate, pinnatifid or pinnatisect, apex conform, abaxially with small scales, brown, triangular-lanceolate; *rachises* grooved adaxially, abaxially with scales similar to those on the lamina, *pinnae* tapering towards the base, the middle ones 0.2–0.7 x 1–3 (7) cm, *costae* grooved adaxially, prominent abaxially, *veins* free, simple or 1-furcate, catadromous, ending in submarginal patent hydathodes; *fertile fronds* distinctly longer than sterile ones, (19) 40 (67) cm long, *stipes* light brown or green, 2–5 (14) cm, *laminae* linear to elliptic-lanceolate, 13–35 (54) cm, with scales on the abaxial side of the lamina and rachis like those of the sterile fronds; *pinnae* contracted, the middle ones 0.1–0.4 x 1.5–3 (5) cm; *sori* linear, continuous, forming coenosori on both sides of costa, occupying entire length of pinna, not decurrent towards rachis; *indusia* brown, continuous, long and coiled; *sporangia* with 19–20 arc cells; *spores* monolete, 30–55 x 50–70 μm, perisporium brown, surface granularly reticulate.

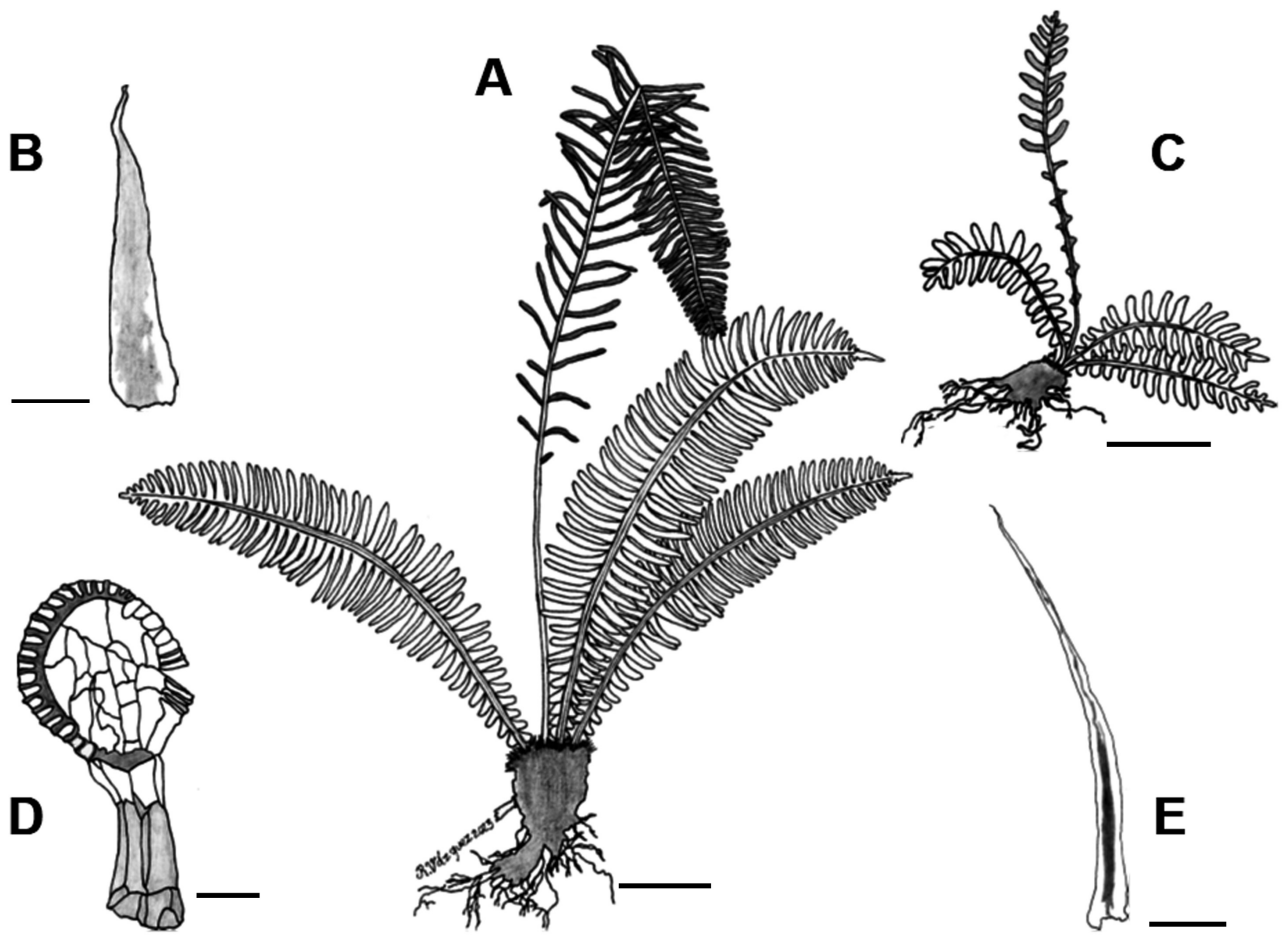


FIGURE 13. Illustration of *Spicantopsis niponica*. A. Habit of *S. niponica* var. *niponica* (J. Umemura 37, P01406521); B. Rhizome scale of *S. niponica* var. *minima* (M. Tagawa 853, P00748579, isotype); C. Habit of *S. niponica* var. *minima* (M. Tagawa 853, P00748579, isotype); D. Sporangium of *S. niponica* var. *niponica* (B. Estébanez s.n., MACB110657); E. Rhizome scale of *S. niponica* var. *niponica* (Maximowicz s.n., S2145). Scale: 4 cm in A; 500 μm in B; 4 cm in C; 100 μm in D; 1.5 mm in E.

Habitat and distribution:—Endemic to Japan. Throughout Japan, from Hokkaido to Yakushima (Kyushu) (Figure 7) (Iwatsuki 1992, Iwatsuki *et al.* 1995). On village roadsides and cleared fields at the foot of hills (Iwatsuki 1992) as well as in montane forests (Ohwi 1953). 60–1600 m.

Chromosome number:— $2n = 62$, diploid (Fabbri 1965, Nakato 1987).

Etymology:—The epithet *niponica* refers to Japan, where the plant is native. Sometimes the specific epithet is found as *nipponica*. This spelling is not correct as both in the original publication of *Spicantopsis niponica* (Nakai 1933) and in the basionym *Lomaria niponica* (Kunze 1848: 508) is found with a single p.

Vernacular name:—Shishigashira (シシガシラ, Japanese) (Iwatsuki 1992). The vernacular name “shishigashira” means “lion head”, probably referring to the rhizome scales, which remain of male lion hair.

Taxonomic notes:—This species closely resembles *Spicantopsis hancockii*, however it differs in some aspects (see section on *S. hancockii*), of which the most reliable seems to be the presence of two posterior cells in the sporangium of *S. niponica*, absent in *S. hancockii*. Moreover, recent studies have shown that these two species do not coexist, *S. niponica* being a Japanese endemic and *S. hancockii* a Taiwanese endemic. It is also similar to its congener *S. amabilis*, but the size of the plant and differences in the rhizome scales easily separate them (see *S. amabilis* section).

Several forms have been recognized in Yakushima (see synonyms section), where its other variety, *Spicantopsis niponica* var. *minima*, was also described, which shows that it is a species with high phenotypic variability (Iwatsuki 1992). The *niponica* variety can be easily distinguished from the *minima* variety by its size, with *S. niponica* var. *minima* not exceeding 15 cm.

The original material cited in Kunze (1848) is: Japonia. Göring s.n., no date (Herb. Klenz. Lucaean. et proprium). Kunze’s herbarium was deposited in Leipzig (LZ) and mostly destroyed during the Second World War, as confirmed by LZ staff and as stated in Thiers (2024. Continuously updated), making the designation of a neotype necessary. In

the absence of a specific *locus classicus*, we have selected one of the specimens cited by Nakai in his combination *Spicantopsis niponica* (Nakai 1933) as a neotype: *J. Nikai 12* (TI00274317).

Additional specimens examined:—**JAPAN. Hokkaido.** no date, *no collector s.n.* (TI00274319! photo); no date, *N.C. Wright s.n.* (US bc01527323!). **Pref. Hokkaido:** forest reservation near Sapporo, September 1929, *P.H. Dorsett & W.J. Morse 1038* (NL3527438! photo; US1577946!); Ishikari, Sapporo, illegible date, *R. Yatabe* (TI00274318! photo); Ishikari, Sōnkyōu, June 1879, *T. Nakai s.n.* (TI00274320! photo); Mt. Yotei, lake Hangetsu, 2 August 1945, *M. Mizushima s.n.* (TI00274329! photo); Ori river, Homme, Shimamaki-mura, Shimamaki-gun, Shiriboshi-shicho, 3 August 1980, *M. Kato & D.E. Boufford 1581* (GA088401! photo); Oshima, 25 July 1931, *illegible collector 222* (TI00274262! photo); Oshima, Hakodate, 4 August 2008, *Y.-M. Huang s.n.* (TAIF297604! photo); *Ibidem* (TAIF297605! photo); Sapporo, 12 October 1903, *S. Arimoto s.n.* (MO1877400!); *Ibidem*, September 1929, *P.H. Dorsett & W.J. Morse 1038* (P01575938!). **Honshu.** 1866–1871, *Kramer 2280* (P01406581!); 1866, *Tschonoski s.n.* (P01406591!); *Ibidem* (P01406593!). **Pref. Aichi:** Kitashidara-gun, Shidara-machi, 13 August 1977, *J. Murata 4106* (TI00274391! photo); Omoteyama, 7 August 1931, *T. Nakai s.n.* (TI00274314! photo). **Pref. Akita:** Betsudake, Nishikurosawa, 24 June 1946, *T. Yamazaki s.n.* (TI00274349! photo); Okachi-gun, Okachi-machi, Matsunoki pass, 8 October 1972, *H. Kanai & Y. Tateishi 1110* (TI00272835! photo; US2740562!). **Pref. Aomori:** 1866, *J. Faurié 146* (P01406584!); Agamushi, 12 November 1912, *J. Faurié 12* (NY04179851!); *Ibidem*, 12 November 1913, *J. Faurié* (P01406533!); Aomori-ken, Bonjusan northwest of Daishaka, 24 August 1928, *R.K. Beattie & Y. Kurihara 10212a* (US2292145!); *Ibidem*, *R.K. Beattie & Y. Kurihara 10312* (US2292144!); Hakkoda, no date, *no collector s.n.* (TI00274345! photo); Kamikita Dist., Towada, 2 November 1946, *U. Narita 555* (TI00274339! photo); Mutsu, Mt. Hakkoda, 31 July 1926, *S. Hattori s.n.* (TI00274316! photo); Towada, 26 June 1894, *E. Drake & J. Faurié 13280* (C0364773F!; C0364775F!; P01406585!). **Pref. Fukui:** Echizen, Nanjo Nagono, 26 July 1933, *Y. Hosoi 151* [interpreted] (TI00272857! photo). **Pref. Chiba:** Tsui, Komachi, Shimoso, Tsuba, Ichikawa, Matsu, 14 July 1963, *H. Ohba 418* (TI00274400! photo). **Pref. Fukushima:** Aizu, the foot of Mt. Bandai-san, 3–4 November 1967, *H. Ohba 671116* (TI00274384! photo); Hanami Yama, 1866–1871, *L. Savatier s.n.* (P01406583!); Haramachi-shi, 16 December 2004, *K. Iga 24* (TI00203872! photo); hills north of Hamata, 24 August 1927, *R.K. & Y. Kurihara 10047* (US2292107!); Iwashiro, 14 July 1940, *T. Nakai s.n.* (TI00274279! photo); Iwashiro, Adizu, August 1879, *R. Yatabe & J. Matsumura s.n.* (TI00274323! photo); Kaihozan, 1 October 1949, *H. Uematu 1780* (TI00274360! photo); Nishishirakawa, Furomuraya, 24 May 1930, *H. Sakaki 54* (TI00274269! photo); Yama-gun, Yamato-machi, Ichinoki, 28 August 1980, *H. Ohba & S. Akiyama 1867* (TI00274294! photo). **Pref. Gifu:** Mt. Kinka, 1 November 2010, *W.-L. Chiou 15469* (TAIF462180! photo; TAIF462184! photo); Ono, Miwa Sanctuary, 8 June 1886, *S. Tanaka s.n.* (TI00272845! photo). **Pref. Gunma:** Kōdzuke, circa cataractum Ogura, Shima, August 1929, *T. Kondō s.n.* (TI00274330! photo); Kusatsu, September 1877, *Dickim* [interpreted] (P01406587!); Mt. Akagi, November 1934, *S. Adachi 28* (TI00272855! photo); Takasaki-shi, Mt. Kan'nonyama, 23 December 1966, *H. Ohba 662135* (TI00274385! photo); Tano-gun, Ueno-mura, Otchizawa, 15 July 1976, *J. Murata 2252* (TI00272859! photo); Tano-gun, Ueno-mura, Yaegoya, Jukkoko tooge, 8 September 1976, *J. Murata 2824* (TI00272860! photos). **Pref. Hiroshima:** Saiki-gun, Itsukaichi, Mt. Madogayama, Ugiri valley, April 1971, *T. Koponen & A. Koponen 16808* (H1675159! photo); *Ibidem*, *T. Koponen & A. Koponen 16817* (H1675149! photo); Tentokukyo, 1936, *illegible collector* (TI00274280! photo). **Pref. Hyogo:** Awaji, Toda, 6 August 1948, *A. Ishigami s.n.* (TI00274369! photo); Hikami-gun, Mt. Myoko-san, 23 September 1960, *M. Tagawa & K. Iwatsuki 3014* (TI00274394! photo); Kawakami, Oogochicho, Kanzaki-gun, 26 July 1965, *K. Iwatsuki 6988* (US2424173!); Mt. Myōkō-san, Hikami-gun, 23 September 1960, *M. Tagawa & K. Iwatsuki 3014* (P01575937!; US2423733!); Yamamoto in Sottsu, 10 February 1953, *N. Togasi 710* (TI00274366! photo); Yamamoto, Takarazuka, 28 July 1962, *M. Togashi s.n.* (TI00274395! photo). **Pref. Ishikawa:** Keta Sanctuary, 29 June 1952, *N. Satomi s.n.* (TI00272853! photo); Komatsu-shi, Sawa-machi, 22 August 1994, *K. Yonekura 3331* (MO04989202!); Mt. Sekido, 26 June 1972, *M.T. Kao 8405* (NY04179848!); Noto, Minani, 11 July 1931, *H. Hara s.n.* (TI00274258! photo); Noto, Ushitsu, Yaho, 13 February 1931, *H. Hara 95* (TI00274256! photo). **Pref. Iwate:** Nishiiwai Gun, Hiraizumi Machi, Motsuji Temple, 1 November 2018, *W.-C. Hsu 72* (TAIF522703! photo). **Pref. Kanagawa:** 25 October 1889, *no collector* (TI00274374! photo); Hakone, July 1869, *Drake 1558* (P01406579!); Hakone, 1866–1974, *M. Savatier 1558* (US483272!; US bc05127319!); Hakone, Atami michi, 26 December 1886, *no collector s.n.* (TI00274284! photo); Hakone, Komagatake, 1 August 1906, *H. Sakurai s.n.* (P01406576!); Hakone, Sagami, 21 October 1902, *M. Weigel s.n.* (P01406578!); *ibidem*, August 1904, *T. Makino s.n.* (TI00274285! photo); Kantō, Yokohama, 1862, *Maximowicz s.n.* (NY04179855!); *Ibidem* (P01406592!); Sagami, 24 July 1962, *H. Ohba 10911* (TI00274299! photo); Sagami, Tanzawa, 22 July 1942, *illegible collector 10814* (TI00274298! photo). **Pref. Kyoto:** 1891–1893, *K. Berry s.n.* (MO2817713!); Canyon on Otani-yama back of Oji, Tamba, 2 November 1927, *R.K. Beattie & Y. Kurihara 10128* (US2292118!); Chohroh-ga-take (Mount Chorogatake), 9 September 1979, *Y. Saiki 1022* (C0364727F!); Fushimi Inari Taisha Shrine, 6 October 2015, *C.-W.*

Chen Wade4529 (TAIF500147! photo); Hozu-chō, Kameoka-shi, 14 September 1987, *T. Takahashi 423* (MO3893847!); Kitakuwada, Chii, Experimental Forest of Ashio University, 17 July 1940, *T. Nakai s.n.* (TI00274277! photo); Kurama, November 1895, *no collector* (NY04179857!); Miyama-cho, Ashiu, Kyoto University Forest Reserve, 19 September 1996, *H. van der Werff 14052* (MO0536479!); mountain back of Miyako Hotel, 25 May 1929, *R.K. Beattie & Y. Kurihara* (US2292160!); Ohmi, Mt. Hiei, 11 September 1966, *van Steenis s.n.* (NL3527437! photo); Sakura-toge, Higashibetsuin-cho, Kameoka-shi, 16 August 1991, *T. Takahashi 2060* (MO4029368!); Sakyo-fu, tributary of Kitashiro-gawa river, SW side of Mt. Hiei-zan, 19 June 1977, *D.E. Boufford & E.W. Wood 19188* (NL984166232! photo); Shishigatani, 30 October 1955, *M. Tagawa 7150* (P01608625; TI00274305! photo; US2420041!); Tango, August 1905, *K. T. Tanaka s.n.* (TI00274292! photo); Yokosuka, 1866–1871, *A. Henschel 1558* (P01557335!). **Pref. Mia:** Iga, Ishiharadani, 8 August 1880, *J. Matsumura s.n.* (TI00272842! photo); Ise, Mt. Tarusakayama, 24 August 1920, *K. Murata 41* (TI00272849! photo); Kitamuro-gun, Yamami-machi, near Kozu-gawa river, 26 July 1981, *S. Akiyama 481* (TI00274306! photo); Mita Zinsya, north of Ueno, 2 August 1954, *M. Tagawa 5928* (US2259007!). **Pref. Miyagi:** Kinkasan, 20 August 1965, *H. Ohba 1728* (TI00272834! photo); Momou-gun, Okachi-machi, Togezahe, 7 February 1989, *T. Kawahara 5606* (TI00274226! photo); Rikuzen, Mt. Funagata, 22 November 1974, *M. Takahashi s.n.* (MO2321470!); *ibidem*, 9 July 1972, *H.S. Ogura 3538* (TI00274265! photo); Rikuzen, Mt. Kattadake, 16 August 1898, *Y. Yabe s.n.* (TI00274344! photo); Sendai-shi, Toshogu, 19 September 1915, *Y. Ogura s.n.* (TI00274393! photo); Tamatsukuri-gun, Narugo-machi, Onikobe Spa, 28 August 1970, *H. Ohba et al 708215* (MO2373914!). **Pref. Nagano:** Kiso-gun, Ookuwa-mura, 14 August 1977, *J. Murata 4156* (TI00274392! photo); Nakamachi, 29 September 1950, *K. Sato 380* (TI00274378! photos); Nishichikuma-gun, Ookuwa-mura, along the river Aderagawa, 14 June 1979, *J. Murata 7720* (TI00274301! photo); Nishikoma, 23 June 1972, *M.T. Kao 8315* (NL996175225! photo; NY04179847!); Oomachi-shi, Taira, West of Lake Aoki, 20 August 1979, *H. Ohba & S. Akiyama 543* (TI00274387! photo); Shinano, Minamisaku-gun, June 1938, *K. Sato 1419* (TI00274377! photo); Shinano, Shimoina, Kazekoshi, August 1940, *J. Furusaura s.n.* [interpreted] (TI00274397! photo); Shinnoa, Kiso, Mt. Ontake, August 1910, *G. Koidzumi s.n.* (TI00274273! photo); Shinnoa, Mt. Yarigatake, July 1920, *T. Nakai s.n.* (TI00274254! photo); Shinnoa, pede montis Yatsugatake, no date, *T. Kondō 28* (TI00272850! photo); Shinnoa, Wadatōge, 24 July 1880, *J. Matsumura s.n.* (TI00274282! photo); Shinnoa, Zenkōji, 9 July 1884, *J. Matsumura s.n.* (TI00274355! photo); Shinshu, no date, *Kondo 28* (TI00274272! photo); *ibidem*, August 1933, *H. Isu s.n.* (TI00274276! photo); *ibidem*, 14 August 1933, *S. Momose s.n.* (TI00272848! photo); *ibidem* (TI00272852! photo); *ibidem*, 15 August 1933, *S. Momose s.n.* (TI00272851! photo); *ibidem*, November 1933, *Ikane* [interpreted] (TI00274281! photo); *ibidem*, 25 July 1939, *S. Gomi 4* [interpreted] (TI00272856! photo); Shinshu, Ushibo, Onsen, 19 January 1933, *S. Momose s.n.* (TI00272847! photo). **Pref. Nara:** 13 September 1993, *И.М.Красноборов & М.Н. Ломоносова s.n.* (NS0009500! photo); 27 May 1929, *P.H. Dorsett & W.J. Morse 711* (US1577934!); gorge of the Sannoko, Kawakami-mura, Yoshino-gun, 7 October 1954, *M. Tagawa 6701* (US2259054!); Kamikitayama-mura, Yoshino-gun, en route from Mt. Wasamata to Mt. Daifugen, 21 September 1986, *S. Tsugaru et al 7443* (MO4012484!; NY4179846!); Mt. Kasuga, October 1921, *T. Makino 41289* (TI00274286! photo). **Pref. Niigata:** Minamikanbara-gun, Shimota-mura, near Nagasawa, 17 August 1980, *H. Ohba & S. Akiyama 1746* (TI00274296! photo); Nakasatomura, 19 September 1982, *T. Takahashi 5538-3567,6644* (TI00138456! photo); Niitsu-shi, 11 October 1982, *T. Takahashi 5639-4089, 6726* (TI00139368! photo); Oguni-achi, 11 September 1983, *T. Takahashi 5538-7563, 7012* (TI00221055! photo). **Pref. Okayama:** 14 October 1925, *no collector 10220* (TI00274275! photo). **Pref. Okayama:** Maniwa, Kawakami, 2 June 1930, *Secondare School of Tokuda s.n.* (TI00274333! photo). **Pref. Osaka:** Yamamoto, Sottsu, 10 February 1953, *N. Togashi 710* (S2061!). **Pref. Saitama:** beside Akasawa Valley, the deepest branch of Arakawa River, Kawamata, Ohtaki-mura, Chichibu-gun, 1 August 1963, *H. Ohba 535* (TI00274295! photo); between Kabagoya and Karisaka-pass, Mts. Chichibu, Ohtaki-mura, Chichibu-gun, 4 August 1963, *H. Ohba 562* (TI00272833! photo); Kamikawa Division, Asahikawa City, Kaguraoka, 25 July 1924, *S. Saito s.n.* (TI00274381! photo); Mt. Hidaka, August 1928, *T. Nakai s.n.* (TI00274309! photo); Musashi, Mt. Bukōsan, 31 March 1908, *T. Nakai s.n.* (TI00274315! photo). **Pref. Shiga:** Ueno Tsuchiyama (Moji), 24 April 1942, *T. Hashimoto 286* (TI00272836! photo). **Pref. Shimane:** Izumo, 5 November 1904, *K. Hirata 34* (TI00274268! photo); Mt. Daimanji, Oki Islands, 23 July 1932, *Y. Nozu s.n.* (TI00274379! photo). **Pref. Shizuoka:** Izu, Kamo Dist., Minaitsuchi, 28 August 1943, *Y. Kimura s.n.* (TI00274365! photo); Izu lake, Yugashima (Mukai, Taira) 11 November 1946, *T. Harada 843* (TI00274335! photo); Izu, Mikurajima, October 1932, *Takashi s.n.* (TI00274367! photo); Mt. Fuji, 1924–1926, *B. Hayata s.n.* (TI00272840! photo); Prov. Totomi, the side of Mt. Hakkozan, Oshiro National Forest, Haibara-gun, 16 September 1967, *H. Ohba 3553* (TI00274388! photo; TI00274389! photo; TI00274390! photo); Toi River, Toi-cho, Kameda-gun, Oshima-shicho, 26 July 1980, *M. Kato & D.E. Boufford 1978* (GA088400! photo); Totomi, Nishikashima, Tenryu-shi, 17 June 1961, *K. Satake s.n.* (US2979919!); Umegashima-mura, Abetoge, 3 August 1959, *Y. Asai s.n.* (TI00274288! photo). **Pref. Tochigi:** Mt. Nasu Daimaru hot spring Shimotsuke, 15 July 1953, *T. Namegata 3149*

(US2138707!); Nikko, no date, *Ito s.n.* (TI00274352! photo); *ibidem* (TI00274353! photo); Nikko, 10 September 1808, *Y. Numajiri s.n.* (TI00274372! photo); Nikko, July 1937, *J. Furusawa s.n.* [interpreted] (TI00274371! photo); Shimotsuke, Mt. Nasusan, 12 August 1908, *W. Sakourai s.n.* (P01406595!); *Ibidem*, 16 August 1911, *no collector* (US1095352!); Shimotsuke, 3 July 1933, *H. Ito s.n.* (TI00274308! photo); Shimotsuke, Nikko, 1 August 1877, *J. Matsumura s.n.* (TI00274327! photo); Shimotsuke, Shimotsuga-gun, Kawakayama, 2 October 1938, *T. Maekawa 80222* (TI00274368! photo). **Pref. Tokyo:** Bushu, Tama village, 12 August 1946, *M. Mizushima s.n.* (TI00274337! photo); Izu Islands, Island Hachijo-jima, in the crater basin of Mt. Hachijo-fuji Hachijo-cho, 6 November 1977, *M. Kato & E. Miki 43* (TI00274264! photo); Izu Islands, Island Mikura-jima, July-August 1967, *H. Ohba 677185* (TI00274293! photo; US2598946!); *Ibidem*, 28 July-4 August 1967, *Y. Jotani et al. s.n.* (TI00274399! photo); Izu Islands, Island Miyake, 14–16 April 1983, *N. Murakami s.n.* (TI00272861! photo); Island Nijima, Mt. Mukai, 12 June 2004, *T. Miyazaki N4050* (TI00274382! photo); Nishitama, Mt. Atago, 10 November 1950, *M. Mizushima s.n.* (TI00274270! photo); Oyama, Miyakejima, 26 August 1979, *no collector* (TI00274267! photo). **Pref. Tottori:** Hino-gun, Nichinan-machi, Nr. Shimoabire, 9 September 1980, *H. Ohba & S. Akiyama 2191* (TI00274297! photo); Tottori-shi, 17 July 2017, *B. Estébanez s.n.* (MACB110656!). **Pref. Toyama:** Mugiton, October 1885, *Y. Etsu s.n.* (TI00272858! photo); Neigun, Yatsuo Machi, Tochiori, 12 October 1990, *J. Jutila et al. 239* (MO4380674!); Takano, Tosa, Takaoka, illegible date, *K. Yana s.n.* (TI00274336! photo). **Pref. Yamagata:** 23 July 1942, *Yamazaki s.n.* (TI00274347! photo); Mikawa, Okazaki, 5 October 1911, *J. Umemura 37* (P01406521!); Nakayama, Miki-cho, Kida-gun, Kagawa, 5 August 1957, *H. Kawasaki s.n.* (TI00274340! photo). **Pref. Yamaguchi:** Kika Park, East slope of Castle Mountain (Shiroyama) National forest, west bank of Nishiki River, Yokoyama village in Iwakuni City. (25.6 miles west of Hiroshima City), 4 October 1953, *L.A. Charette 1441* (US2256115!; US2357200!). **Pref. Yamanashi:** Kaikoma, 16 July 1946, *H. Nematsu s.n.* (TI00274362! photo); Kai, Mitsutoge, 29 August 1936, *K. Hiyama 7760* (TI00274338! photo); Kai, Nanri, March 1949, *H. Nematsu s.n.* (TI00274361! photo). **Pref. Wakayama:** Hidaka Dist., August 1928, *T. Nakai s.n.* (TI00274311! photo); *ibidem* (TI00274312! photo); *ibidem* (TI00274313! photo); Hidaka Dist., Samukawa, August 1920, *no collector s.n.* (TI00274271! photo); Kii, Nachi, June 1926, *T. Nakai s.n.* (TI00272838! photo; TI00272839! photo; TI00274255! photo; TI00274357! photo); Kii, Wakanoura, 5 January 1878, *J. Matsumura s.n.* (TI00272843! photo); Koya-san, 23 June 1929, *R.K. Beattie & Y. Kurihara 10835* (US2292165!); Tanabe-shi, Nakahechi-cho, Mizukami, 21 August 2017, *B. Estébanez s.n.* (MACB110657!). **Kyushu.** North Kyūshū, September 1933, *R.K. Smith 20* (US1756269!). **Pref. Fukuoka:** Kokura, August 1929, *T. Kondo s.n.* (TI00274331! photo); Nanokawa, Tosa, 29 July 1892, *no collector* (US bc01527320!). **Pref. Kagoshima:** Amagi, 28 December 1890, *no collector* (P01406575!); Amagi, 21 October 1944, *Y. Yamazaki s.n.* (TI00274348! photo); Amagi, 9 October 1956, *Owi & Okamoto 1402* (P01406594!); Amagi, MT. Douzhou, 10 June 1883, *no collector s.n.* (TI00272841! photo); Hanamaki, Inaodake, 14 July 1967, *Y. Ando s.n.* (TI00274398! photo); Kirishima, 10 August 1886, *S. Tanaka s.n.* (TI00272844! photo); Kirishima, 10 August 1938, *Department of Agriculture Sciences 4* (TI00272837! photo); Mt. Amagi in Idzu, 9 October 1956, *J. Ohwi & K. Okamoto 1402* (H1127512! photo; NY04179849!; TI00274263! photo; US2259137!); Ôsumi, Mt. Kirishima, 5 August 1882, *R. Yatabe & J. Matsumura s.n.* (TI00274321! photo); *ibidem*, 29 August 1890, *S. Tanaka s.n.* (TI00272846! photo); Yakushima Island, 16 July 1922, *G. Masamune s.n.* (NY04179853!); *Ibidem*, 23 September 1984, *D. Sather & G. Caddell 6441* (NCU00348585! photo); Yakushima Island, around Sandaisugi and Kosugidani, 17 July 1984, *M. Kato et al. 17-19* (TI00274307! photo); Yakushima Island, Hananoegoo, 6 August 1961, *M. Furuse 38848* (TI00274304! photo); Yakushima Island, Prov. Ohsumi, 27 December 1961, *S. Kurata 6110* (US2979912!); *ibidem* 29 July 1924, *G. Masamune* (TI00274375! photo); Yakushima Island, Sandaisugi, Kosugidani Valley, 30 March 1966, *H. Ohba 662558* (TI00274386! photo); Yakushima Island, Yaku-cho, Hana-yama, Okawa-rindo, 12 October 1977, *D.E. Boufford 20171* (MO2609648!). **Pref. Kanagawa:** Sagami, Hakone, August 1926, *T. Nakai s.n.* (TI00274253! photo). **Pref. Kumamoto:** Fukurengi, Tsunoyama, 3 April 1932, *H. Hara 437* (TI00274257! photo); Hondo, Yamamoto in Sottsu, 10 February 1953, *H. Togasi 710* (H1127514! photo; H1127515! photo; US2136494!); Mizukami, 19 October 1928, *H. Hara s.n.* (TI00274261! photo). **Pref. Nagasaki:** 1863, *Maximowicz s.n.* (S2144!); Hizen, May 1879, *R. Yatabe & J. Matsumura s.n.* (TI00274356! photo); Hizen, Mt. Unzen, 6 July 1913, *B. Hayata s.n.* (TI00274341! photo); Unzen National Park, growing on Mount Kunimidake, 28 September 1983, *D. Sather & G. Caddell 3026* (NCU00348584! photo). **Pref. Ooita:** Aso National Park, growing on Mount Kuju along trail from Chojobaru, 9 May 1983, *D. Sather & G. Caddell 2517* (NCU00348583! photo); Takeda-shi, Shirouzu, Ooshoojiwa (Mts. Sobo-Katamuki), 7 July 1979, *J. Murata 7979* (TI00274302! photo). **Pref. Saga:** Mt. Kurokami, August 1950, *T. Hashimoto 790* (TI00274334! photo); **Shikoku.** **Pref. Ehime:** Iyo Prov., Mr. Onigajyō, 8 June 1927, *T. Nakai s.n.* (TI00274252! photo; TI00274358! photo; TI00274359! photo). **Pref. Kochi:** Hata Distr., Kuroshio Town, Tachibana-gawa, Kami-Nadayama national forest, 26 October 2010, *T. Miyazaki 1011857* (TI00274364! photo); Nagaoka-gun, Ootoyo-machi, Mt. Kajigamori, 15 August 1961, *K. Oonishi 289344* (TI00274363! photo); Takaoka District, Naro, Kubokawa Town,

10 August 2005, *T. Miyazaki 508123* (TI00274290! photo); Takaoka District, Natsugare Pass, Nakatosa Town, 7 August 2005, *T. Miyazaki 508017* (TI00274289! photo); Takaoka District, Sakawa-Cho, 19 September 1985, *N. Inagaki M85-237* (TI00274287! photo); Takaoka District, Shimanto Town, Shiwamine, 1 November 2010, *T. Miyazaki 1011239* (TI00274291! photo); Takaoka District, Shuujuin, Kubokawa Town, 10 August 2005, *T. Miyazaki 508146* (TI00274383! photo); Tosa, July 1889, *Christ s.n.* (P01406589!); Tosa, Mt. Ushioe, 4 January 1939, *H. Itô s.n.* (TI00274350! photo); Tosa, Tosa-gum, Tosayama-mura, 8 June 1931, *H. Itô s.n.* (TI00274278); Ysgi, Asagun, Aki, 8 August 1932, *T. Tsuyama* (TI00274396! photo). **Pref. Tokushima:** Awa, Mt. Ôyama, no date, *J. Nikai 2320* (TI00274354! photo); Mt. Tsurugisan, Nishijimajinja-Taikenjinja, 4 October 1978, *J. Murata 6567* (TI00274300! photo); Awa, oppido Shimomoyô, 25 July 1888, *R. Yatabe* (TI00274322! photo). **Unknown location:** no date, *no collector* (P01406582!); *ibidem* (TI00274370! photo); *ibidem* (TI00274346! photo); no date, *no collector 345* (TI00274343! photo); illegible date, *no collector s.n.* (TI00274324! photo); *ibidem* (TI00274325! photo); *ibidem* (TI00274326! photo); *ibidem* (TI00274328! photo); no date, *A.W. Stanford s.n.* (C825009F!); *Ibidem* (NY04179856!); no date, *Y. Yoshii s.n.* [interpreted] (TI00272854! photo); 1866–1871, *illegible collector* (P01619264!); 1866, *Tschonoski s.n.* (NY04179852!); 1888, *H. Matzumo 12998* [interpreted] (P01619263!); May 1888, *no collector* (US bc01527324!); June 1896, *M.L. Holbrook 177* (NY04179854!); 8 October 1899, *Baker 178* (MO1877401!); 25 August 1905, *H. Sakurai 1912* (H1127513! photo); 20 August 1913, *no collector* (P01406574!); 18 September 1921, *no collector* (TAIF50586! photo); no date, *J. Matsumura 48* (P01619262!); 12 August 1908, *L. Sakurai s.n.* (NY04179850!); 9 February 1910, *Christ s.n.* (P01406588!); 12 August 1908, *Nerville s.n.* (P01571953!); August 1928, *T. Nakai* (TI00274310! photo); 22 July 1931, *H. Muramatsu s.n.* (TI00274274! photo); Nyokoji [interpreted], 6 August 1934, *K. Ohki s.n.* (TI00274332! photo); 31 January 1937, *I. Simozawa s.n.* (MO5423293!).

Spicantopsis niponica (Kunze) Nakai var. ***minima*** Tagawa (1938: 706) (Figure 13B–C).

Type:—JAPAN. Kyushu, Prov. Osumi, Hananoego, Isl. Yaku-sima, 18 August 1933, *M. Tagawa 853* (KYO not seen, holotype; P00748579!, isotype; US00135467!, isotype).

Synonyms:—≡*Struthiopteris niponica* var. *minima* (Tagawa) Masamune (1951: 198).

Invalid designation: *Blechnum niponicum* var. *minimum* (Tagawa) Nakaike (2013: 23) nom. inval. (basonym ref. incorrect).

Plants terrestrial; *rhizomes* thick, very short, erect, with scales ovo-lanceolate, papyraceous, discoloured, centre broadly sclerotized from base to apex, dark brown, margins lighter brown, entire, 0.3–0.7 x 3–4 mm; *fronds* dimorphic, *sterile fronds* 4–7 cm long, shortly petiolate, *stipes* no longer than 1.5 cm, *laminae* elliptic-lanceolate, coriaceous, 1.5–3 x 5–10 cm, 1-pinnate or pinnatifid, with conform apex, *rachis* grooved adaxially, *pinnae* tapering towards the base, the middle ones 0.15–0.3 x 0.6–1.5 cm, *veins* free, simple or 1-furcated, catadromous, ending in submarginal, patent hydathodes; *fertile fronds* longer than the sterile ones, 6–15 cm long, *stipes* 1–2 cm, *laminae* elliptic-lanceolate, 1–2 x 6–15 cm, 1-pinnate with conform apex, *pinnae* contracted, the middle ones 0.1–0.2 x 0.5–1 cm; *sori* linear, continuous, forming coenosori on both sides of costa, occupying the entire length of the pinna; *indusia* continuous, long and coiled; *sporangia* and *spores* not seen.

Habitat and distribution:—Endemic to Japan (Iwatsuki 1992), originally described as an endemism of the Yakushima Island (Tagawa 1938), but we have found specimens from Kyoto prefecture (Honshu) and Yamagata prefecture (Kyushu). On road slopes and rock crevices. 60–800 m (Figure 7).

Chromosome number:— $2n = 62$, diploid (Shinohara & Murakami 2006).

Etymology:—The epithet *minima* refers to its small size compared to the type variety.

Vernacular names:—Hime-shishigasira (ヒメシシガシラ, Japanese) (Iwatsuki 1992). Hime-shishigasira means something like “princess lion head head”, meaning that it is a small version of the lion head fern (*S. niponica*).

Taxonomic notes:—It can be distinguished from *S. niponica* var. *niponica* by having smaller rhizome, rhizome scales, and fronds, and simpler venation. This variety has been little studied at the anatomical and palynological level because most of the material examined was type material. For this reason, in the study of Molino *et al.* (2019b) it could not be included in the phylogeny, and only two sequences of two markers already deposited in GenBank were available. Therefore, a more detailed study of this variety would be interesting to determine its taxonomic status.

Additional specimens examined:—JAPAN. Honshu. **Pref. Kyoto:** Lom Mio, en exposition SW aux environs du K.I.C.H., 13 July 1969, *H. de Leiris s.n.* (P06491206!). **Kyushu. Pref. Kagoshima:** Yakushima Island, Hananoe, Kawaichi, Kosugi valley, 4 August 1939, *Y. Kimura 39169* (TI00274342! photo); Yakushima Island, Prov. Satsuma, to Shika-no-sawa from halfway-midpart Mt. Nagata-dake, Kami-yaku-choo, 12 October 1963, *M. Furuse 41658* (TI00274303! photo); Yakushima Island, Prov. Osumi, 25 October 1950, *S. Hatusima 14680* (US2138202!); Yakushima Island, Yakumachi, Mt. Motchom (Onoaida-peak-Tanayokehodo-Sempiro Fall), 23 July 1982, *T. Yahara*

et al 6201 (TI00274380! photo). **Pref. Yamagata:** Kaminoyama-shi, N. slope of Dorobu, 23 June 1995, *Y. Endo et al.* 19 (MO05088220!).

***Struthiopteris* Scop.** (Figure 9D–H; Figure 14).

Type:—*Struthiopteris spicant* (L.) Weiss.

Plants terrestrial; *rhizomes* erect, not stoloniferous, dark, covered with linear-lanceolate, triangular-lanceolate, or ovate-lanceolate, concolorous or discoloured, chestnut to dark chestnut scales, with sclerosed centre or not, entire margins or with sparse excrescences; *fronds* dimorphic, subdimorphic (*S. spicant* var. *homophyllum*) or monomorphic (*S. fallax*), *sterile fronds* with *stipes* slender, round in section, short, dark, brown, or black, sometimes atropurpureous, with scales proximally similar to those on the rhizome, glabrous distally, striate or densely to smoothly punctate, *laminae* lanceolate to ovate-lanceolate, 1-pinnate or pinnatifid, gradually reduced towards the base, with glandular hairs on the lamina surface, apices pinnatifid to conform, *rachis* black to dark brown proximally, grooved adaxially; *pinnae* adnate, oblong-linear to linear-falcate, with entire margins; *costae* green, grooved abaxially, prominent adaxially; *veins* free, simple to 1-furcate, catadromous, ending in adaxial submarginal hydathodes, *stomata* aligned following veins on abaxial face of pinnae; *fertile fronds* longer and more erect (in the dimorphic taxa); *stipes* similar to the sterile ones but much longer, sometimes as long as the laminae, *laminae* similar in shape to the sterile ones, but with *pinnae* contracted, with almost not green tissue; *rachises* and *costae* as those in the sterile fronds; *sori* linear, continuous, sometimes interrupted (*S. spicant* var. *homophyllum* and *S. spicant* var. *pradae*), forming coenosori on both sides of costa; *indusia* linear, continuous or not, entire; *sporangia* with 12–20 arc cells in the ring; *spores* monoletate, perispores brown, irregularly folded.

Distribution:—Northern Hemisphere. Northwest America, Europe, the Macaronesian archipelagos and North of Africa and Japan (Figure 1).

Basic chromosome number:— $n = 34$.

Taxonomic notes:—The genus most closely related within the family is *Spicantopsis*. For differences see the Taxonomic notes section of that genus. The other two genera to which it is phylogenetically most closely related are *Brainea* and *Blechnidium* (Gasper *et al.* 2016, 2017, Molino *et al.* 2019b), however, morphologically they are not similar, these genera presenting anastomosing venation (vs. simple venation in *Struthiopteris*). Despite not being phylogenetically closely related, it has some resemblance to some species of the genus *Austroblechnum*, but differs in the margins of the pinnae, which are crenulate to serrate in *Austroblechnum* and entire in *Struthiopteris*, however, this difference is not always clear. They also differ in the spores, since in *Austroblechnum* the perispore is smooth and never has folds, while in *Struthiopteris* is always folded (Moran *et al.*, 2018, Molino *et al.* 2020). In addition, *Austroblechnum* has an austral distribution (Gasper *et al.* 2016), while *Struthiopteris* is only found in temple areas of the North Hemisphere. Also, although phylogenetically distant too, it is very similar to *Cleistoblechnum*. It differs in that the fronds of this genus the margins of the pinnae are strongly revolute (vs. straight in *Struthiopteris*) and the laminae are more coriaceous.

Identification key to *Struthiopteris* species.

1. Fronds dimorphic, subdimorphic or monomorphic, over 5 cm tall. In Europe, North America or Japan 2.
- Fronds monomorphic, with no more than 5 cm tall. Restricted to Iceland *S. fallax*
2. Sterile pinnae rounded; stipes densely punctate in irregular lines; Plants dimorphic; Japan *S. castanea*
- Sterile pinnae acute; stipes striate or smoothly punctate; Monomorphic, subdimorphic or dimorphic plants; Europe and North America 3.
3. Dimorphic or subdimorphic plants with only one sporophyll type 4.
- Dimorphic plants with two types of sporophylls, one longer and more erect than trophophylls and contracted pinnae, and one similar in appearance to trophophylls, but with sori in the middle part of the frond, fragmented towards the base and apex
..... *S. spicant* var. *pradae*
4. Rhizome scales lanceolar-triangular, rarely with sclerosed centre; fronds subdimorphic, not more than 20 cm; sori linear, fragmented *S. spicant* var. *homophyllum*
- Rhizome scales linear, with narrowly sclerosed centre; fronds distinctly dimorphic, up to 100 cm; sori continuous
..... *S. spicant* var. *spicant*

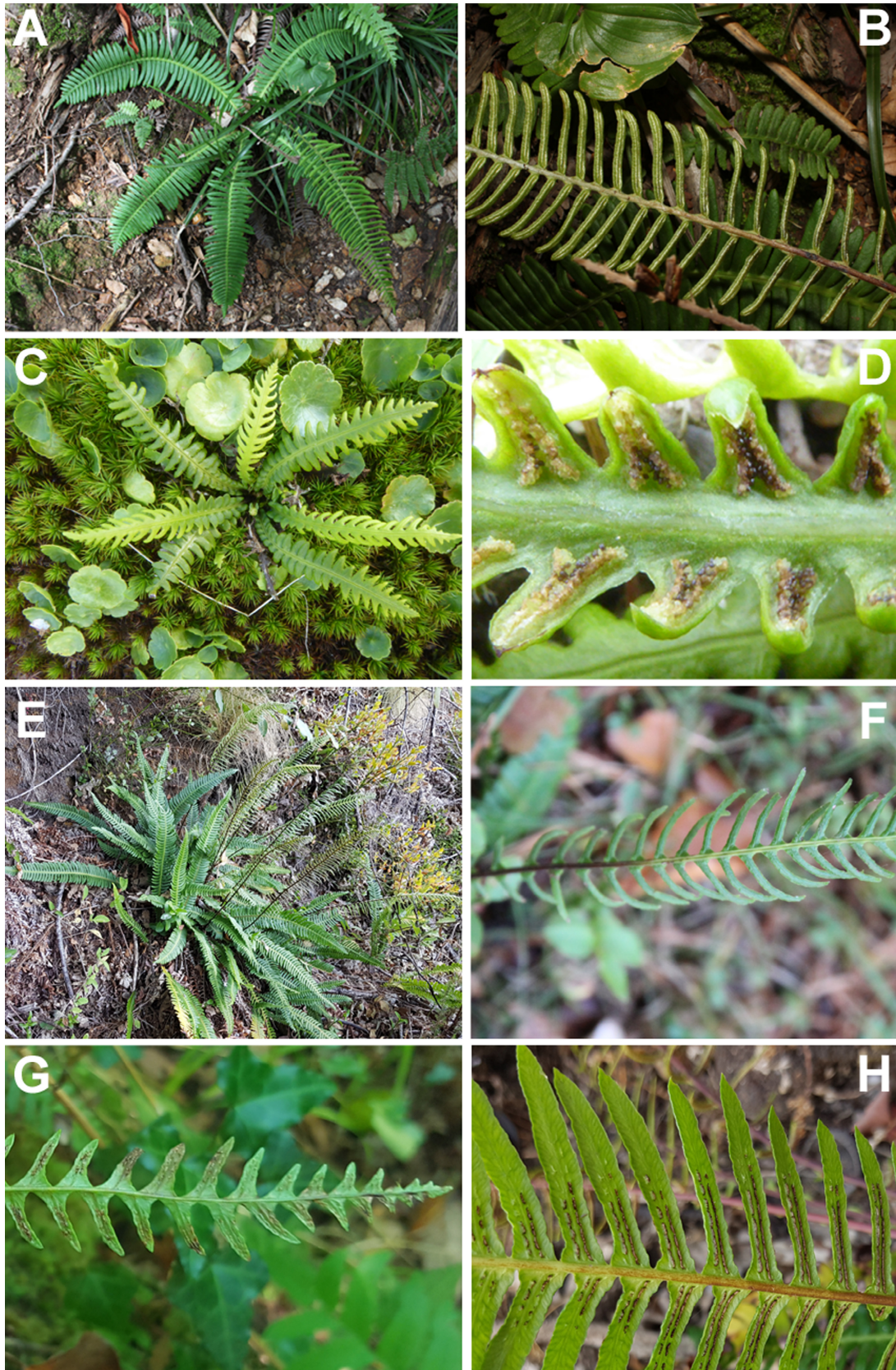


FIGURE 14. *Struthiopteris* species in the field. A-B. *Struthiopteris castanea*. A. Habit; B. Detail of the abaxial side of the fertile frond, bearing sori; C-D. *Struthiopteris fallax*. C. Habit; D. Detail of the abaxial side of the fertile frond, bearing sori; E-F. *Struthiopteris spicant* var. *spicant*. E. Habit; F. Detail of the adaxial side of the fertile frond; G. *Struthiopteris spicant* var. *homophyllum*, detail of the abaxial side of the fertile frond, bearing sori; H. *Struthiopteris spicant* var. *pradae*, detail of the abaxial side of the fertile frond, bearing sori. Pictures: A & B. Shirakawa, Gifu, Japan, by Hiroki Moriwaki; E & H. Zamora, Castilla y León, Spain, by Sonia Molino; F. Soria, Castilla y León, Spain, by Sonia Molino; G. La Coruña, Galicia, Spain, by Sonia Molino.

Struthiopteris castanea (Makino & Nemoto) Nakai (Figure 9D; Figure 14A–B; Figure 15).

Type:—JAPAN. Prov. Rikuzen, Mt. Kurikoma-yama, 25 August 1890, *no collector s.n.* (TNS19854! photo, lectotype, designated in Makino & Nemoto 1925).

Synonyms:—*Blechnum castaneum* Makino & Nemoto.

=*Struthiopteris castanea* (Makino & Nemoto) Nakai var. *viridipes* Honda (1937: 644). **Type:**—JAPAN. Honsyu, Oze, Prov. Iwasiro, 1935, *T. Sakai 1904* (TI not seen, holotype); =*Struthiopteris castanea* (Makino & Nemoto) Nakai f. *viridipes* (Honda) Tagawa (1959: 143).

Invalid designation: Lomaria castanea Makino (1891: 45). nom. nud.

Plants terrestrial; *rhizomes* short, ascending, with brownish scales, linear lanceolate, 0.5–1.5 x 3–8 mm, with the central zone narrowly sclerotized from base to apex, dark brown, entire margins lighter brown; *fronds* dimorphic, *sterile fronds* (13) 25 (41) cm, shortly petiolate, *stipes* dark brown, brown, black or purplish, 0.5–3 (10) cm, *laminae* narrowly lanceolate, 3–6 x 10–40 cm, 1-pinnate or pinnatisect, apex conform, with uniseriate multicellular hairs topped by a red gland of variable size on both sides of the lamina, *rachises* dark brown basally, light brown or green towards apex, grooved adaxially, *pinnae* entire, tapering towards the base, the middle ones 0.3–0.8 x 1–3 cm, rounded and mucronate at apex, *costae* grooved adaxially, prominent abaxially; *veins* free, simple to 1-furcate, ending in adaxial submarginal hydathodes, *stomata* aligned following veins on abaxial face of pinnae; *fertile fronds* up to twice as long as sterile fronds, *stipes* brown, black or purplish, red during growth, 7–12 (20) cm, *laminae* narrowly lanceolate, 2.7–5.2 x 16–44 cm, 1-pinnate or pinnatisect, with uniseriate multicellular hairs topped by a red gland of variable size on both sides of the lamina, *pinnae* contracted, the middle ones 0.1–0.3 x 1–3 cm.; *sori* linear, continuous, forming coenosori on both sides of costa, covering entire length of pinna, decurrent towards rachis; *indusia* linear, continuous; *sporangia* with 16–20 arc cells; *spores* monolete, 40–50 x 50–65 µm, perisporium irregularly folded.

Habitat and distribution:—Endemic to Japan. Occurs from the Tohoku region to the northern tip of Kanto, from Shin-etsu northward, and in San-in from northern Hiroshima Prefecture (Figure 4) (Iwatsuki 1992). Grows in masses in hillside undergrowth in the subalpine zone of Japan. Up to 1,100 m (Ohwi 1953, Iwatsuki 1992, Iwatsuki *et al.* 1995).

Chromosome number:— $2n = 340$, decaploid (Fabbri 1965, Nakato 1987).

Etymology:—The epithet is used to designate chestnut-like colour of the axes (Stearn 1973).

Vernacular name:—Miyama-shishigashira (ミヤマシシガシラ, Japanese) (Iwatsuki 1992). The Japanese name means “lion’s head of Miyama”. Lion’s head (shishigashira) is the name usually given to *Spicantopsis niponica*, presumably because of the similarity of its scales to the mane of a lion. The scales of *Struthiopteris castanea* do not show this effect, but the plant in general resembles *S. niponica*, so we assume that, as it was described later, it was assigned this vernacular because of its similarity to that species. We do not know why it is associated with Miyama, as the original material is not from Miyama.

Taxonomic notes:—This species resembles the representatives of the genus *Spicantopsis* present in Japan but can be easily distinguished by the colour of the stipe, very dark in *S. castanea* and green or very light brown in *Spicantopsis* species. Although it does not cohabit with its congeners, it is actually very similar to *Struthiopteris spicant*, from which it can be distinguished by the ornamentation of the stipe, very densely punctate in *S. castanea* and striate or only slightly punctate in *S. spicant*.

It is common to find specimens of *Lomariidium contiguum* (Mettenius 1861: 70) Gasper & V.A.O. Dittrich in Gasper *et al.* (2016: 212) labelled under the name *Blechnum castaneum* Copeland (1929: 361), as this was an illegitimate name given to this species by Copeland (1929) but was already applied earlier to the present *Struthiopteris castanea*.

The name *Lomaria castanea* Makino has been used as a basionym for *Struthiopteris castanea* on numerous occasions (Ohwi 1953, Tagawa 1959, Nakaike 1975, 1982), but that this is a name that was not validly published as it did not present a description alongside the name (Makino 1892), as has been noted in Molino *et al.* (2019b). In fact, Makino’s next mention of the species is to synonymize it with *Struthiopteris spicant* (sub. *Blechnum spicant*, Makino 1899). A publication by Nakaike (1983) that was overlooked in Molino *et al.* (2019b) confirms this view. It states that, as already indicated by Christensen (1934), the name *Blechnum castaneum* was first correctly published by Makino & Nemoto (1925) with a short description in Japanese. This is confirmed by the finding of the type by Nakaike (1983) in the TNS herbarium, with Nemoto’s handwriting specifying the name *Blechnum castaneum* (TNS19854! photo).

At Oze (National Park in Fukushima, Niigata, and Gunma prefectures, north of Tokyo) a form with green costa, stipe and rachis has been collected and named *Struthiopteris castanea* var. *viridipes*, but it is not a taxon recognized by some authors (Iwatsuki 1992), and we have not found any individuals with these characteristics. The axes of *Spicantopsis niponica* are clearer than in *S. castanea*, and this plant shows a lot of variation (see section on this species), so maybe that collection was a rare specimen of this species.

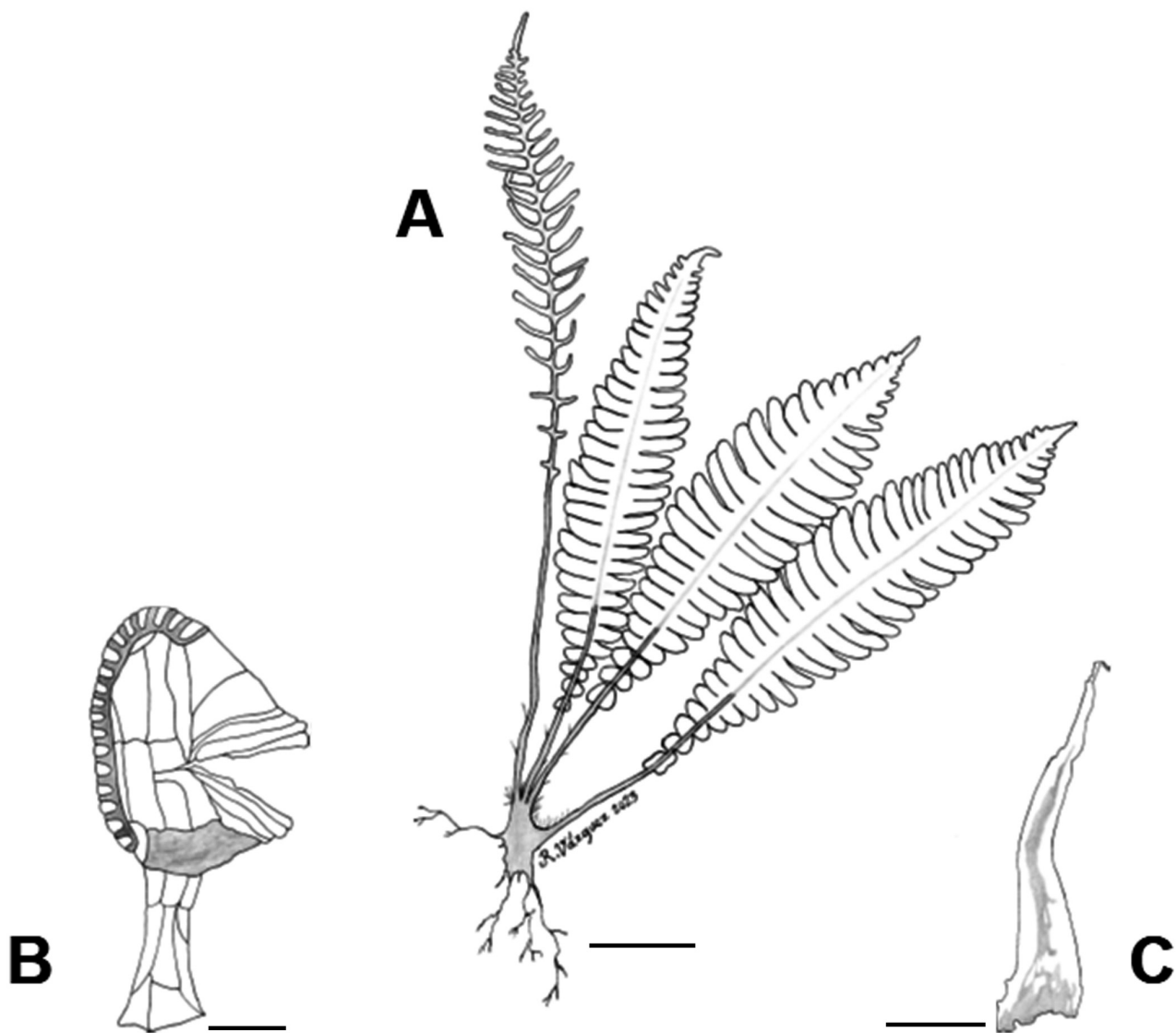


FIGURE 15. Illustration of *Struthiopteris castanea*. A. Habit (no collector, TNS739310); B. Sporangium (M. Mizushima 13,853, S1982); C. Rhizome scale (T. Kawahara s.n., TNS792167). Scale: 4 cm in A; 100 μ m in B; 1 mm in C.

Its chromosomal number, $2n = 340$ (decaploid), is remarkable, being the highest number known for the Blechnaceae family. It is not yet known if this high chromosome number responds to some kind of adaptation, although it is known that this species occupies areas of high altitude, so it could be related to its ability to live in this more hostile territory (Nakato 1987). This chromosomal difference would be expected to be observed in spore size, but the spores of *S. castanea* have been shown to be only slightly larger than those of its tetraploid relatives, *S. fallax* and *S. spicant* (Molino *et al.* 2020).

Additional specimens examined:—JAPAN. Honshu. Pref. Akita: 1927, *Makino 32953* (S1980!). **Pref. Aomori:** Hakkōda, 1861, *Maximowicz s.n.* (S2145!); Hakkōda, Iwakura, 5 September 1959, *K. Iwatsuki 5049* (S1971!; U0043510! photo; US2356861!); Shichinohe-machi, 31 August 1980, *E. Fukushi 8422* (TNS732190!); *Ibidem*, no collector (TNS739308!). **Pref. Fukui:** Imadate-gun, Ikeda-cho, Hekosan, 14 August 1992, *T. Kawahara s.n.* (TNS792167!); Imadate-gun, Ikeda-cho, Kanmuri-yama, no date, *Y. Saito s.n.* (TNS792168!). **Pref. Fukushima:** Hinoemata-mura, 22 July 1934, *S. Okuyama 410* (TNS45261!); Minamiaidu-Gun, Hinoemata-Mura, prope Sanzyo-no-taki, 12 August 1935, *J. Ohwi s.n.* (MICH1613813! photo). **Pref. Iwate:** Isawa-cho, 1 August 1968, no collector (TNS426905!); Shizukuishi-cho, 28 September 1980, no collector (TNS739310!); Wakayanagi-mura, 29 August 1951, *N. Karizumi s.n.* (TNS115371!). **Pref. Gifu:** Ohno-gun, Shirakawa-mura, Sanpoiw adake, 15 August 1992, *M. Murase 5453* (TNS792169!). **Pref. Gunma:** Minakami-mura, 23 August 1894, *K. Watanabe 310* (TNS63209!); Tone-gun, Minakami-chō, Tanigawa Mt., Tenjindaira, Kuma-ana sawa hinangoya, 6 June 2011, *A. Ebihara et al.* 2782 (TNS108194!); Yamanohana-Hatomachi pass, Katashina-mura Tone-gun, 17 August 1974, *K. Suzuki s.n.* (MO249980!).

Pref. Hyogo: Mikana-gun, Onsen-cho, Ueyama-kogen, 25 July 1999, *T. Kobayashi s.n.* (TNS700642!). **Pref. Miyagi:** 5 September 1966, *H. Koyama & F. Konta 1943* (TNS924264! photo). **Pref. Nagano:** Otari-mura, 26 July 1979, *J. Haginiwa 29502* (TNS979502! photo); Otari-mura, 14 September 1985, *M. Futoshi 81107* (TNS832504!); Otari-mura, 27 July 1979, *J. Haginiwa s.n.* (TNS979503!); Shinano, Shumominochi-gun, Minochi-mura, 28 June 1956, *M. Mizushima 13853* (S1982!). **Pref. Niigata:** Ivihirose, 18 August 1949, *Y. Ikegami 13386* (MO5423252!); Koide-machi, 26 August 1967, *Konta 6405* (TNS924267!; TNS924268!); Shibata-shi, 24 October 1963, *F. Konta 3344* (TNS924269! photo); *Ibidem*, 24 December 1963, *F. Konta 3340* (TNS924263!); *Ibidem*, no date, *F. Konta 3350* (TNS924265! photo; TNS924266! photo); Yamato-machi, 8 August 1964, *Y. Ikegami s.n.* (TNS184551!); Yamato-mura, 17 July 1954, *S. Iwano s.n.* (TNS110853!). **Pref. Toyama:** Yatsuo-machi, 15 August 1955, *A. Kirino s.n.* (TNS280676!); Yamagata, Iide-machi, 18 August 1966, *D. Shimizu s.n.* (TNS172556!); *Ibidem* (TNS172559!).

Struthiopteris fallax (Lange) S. Molino, Gabriel y Galán & Wasowicz (Figure 9E; Figure 14C–D; Figure 16).

Type:—ICELAND. Tunguhver, varme Kilde, no date, *Ch. Grønlund s.n.* (C10021769! photo, left hand specimen, i.e., plant no. 2 and its separate parts, lectotype, designated in Wasowicz *et al.* 2017a).

Synonyms:—*Blechnum spicant* (L.) Roth var. *fallax* Lange (1880: 50 [2983]). *Struthiopteris spicant* (L.) Weiss var. *fallax* (Lange) Wasowicz & Gabriel y Galán in Wasowicz *et al.* (2017b: 198).

Plants terrestrial, *rhizomes* short, erect, with lanceolate, concolorous, chestnut-coloured scales, margin entire, 0.3–0.6 x 1.5–2 mm; *fronds* 1–5 cm, monomorphic, forming a rosette above the ground, shortly petiolate, *stipes* 0.1–0.4 cm, brown, black or purplish, *laminae* lanceolate, 0.4–0.7 x 1.3–5 cm, pinnatifid, pinnae tapering towards the base, the middle ones 0.1–0.2 x 0.2–0.6 cm, *rachises* dark basally, green towards the apex, with uniseriate multicellular hairs topped by a red gland; *veins* free, simple or 1-furcate, catadromous, ending in adaxial hydathodes; *sori* linear, continuous, forming coenosori on both sides of costa, occupying the entire length of the pinna; *indusia* linear, continuous; *sporangia* with 13–21 arc cells; *spores* monolet, 20–40 x 30–60 µm, perisporium with marked narrow folds.

Habitat and distribution:—Endemic to northwestern Iceland, at Deildartunguhver hot spring, the biggest hot spring in Europe. Slope in hot spring, whose water is at a temperature of 100°C, and the soil at a constant temperature of 30–40°C (Figure 3) (Wasowicz 2021).

Chromosome number:— $n=68$, tetraploid (Löve & Löve 1966). Tómannson (2016) suggests that this species could be a diploid instead of a tetraploid.

Etymology:—The epithet “*fallax*”, which means deceptive, was given probably because of its deceptive difference from the typical plant (*S. spicant*) (Lange 1880; Löve & Löve 1966).

Vernacular names:—Tunguskollakambur (Icelandic) (Flora of Iceland 2024).

Taxonomic notes:—This species was collected by Grønlund (1881) and cultivated by him in Copenhagen, where it grew with the same characteristics as in nature, which supports its treatment as a distinct species from *Struthiopteris spicant* (Hallgrímsson 1968). This further demonstrated its ability to grow in soils not at the high temperatures of Deildartunguhver, and in fact it has also been grown in the Botanical Garden at Akureyri (northern Iceland) in unheated soil, and in pots in Boulder, Colorado, again growing with the same characteristics as in nature despite differences in climatic conditions (Löve & Löve 1966). Despite its proven ability to grow in colder soils, no other populations have been found elsewhere in Iceland. We do not know the cause of this, but the relatively high proportion of aberrant and aborted spores suggest a lower dispersal power.

In the phylogenetic analyses where it has been included, the species has not been separated from *S. spicant* (Molino *et al.* 2019b, c). However, these were phylogenies based on Sanger sequencing of three chloroplast markers, and in the dating of the genus the divergence between these two species has been shown to be very recent, approximately 0.5 million years, so these analyses may not be sufficient to discriminate both species phylogenetically (Molino *et al.* 2019b). Furthermore, *Struthiopteris fallax* and *S. spicant* are radically different morphologically, anatomically, palynologically, and ecologically, which led to the separation of these two taxa as distinct species (Molino *et al.* 2019c). *Struthiopteris fallax* is a plant with monomorphic fronds, these approximately 5 cm long, whereas *S. spicant* is dimorphic or subdimorphic, with fronds usually 20 cm or longer. Differences have also been found in the shape of the epidermal cells, the cross section of the fertile pinnae and the size of the spores (Molino *et al.* 2019c). They also have a clearly differentiated niche, and it has been shown, as discussed above, that when *S. fallax* spores are grown in environments other than their natural habitat, they grow with the same characteristics. No hybrids have been found between *Struthiopteris fallax* and *S. spicant*, probably because, although both species occur in Iceland, the populations are far apart (Löve & Löve 1966).

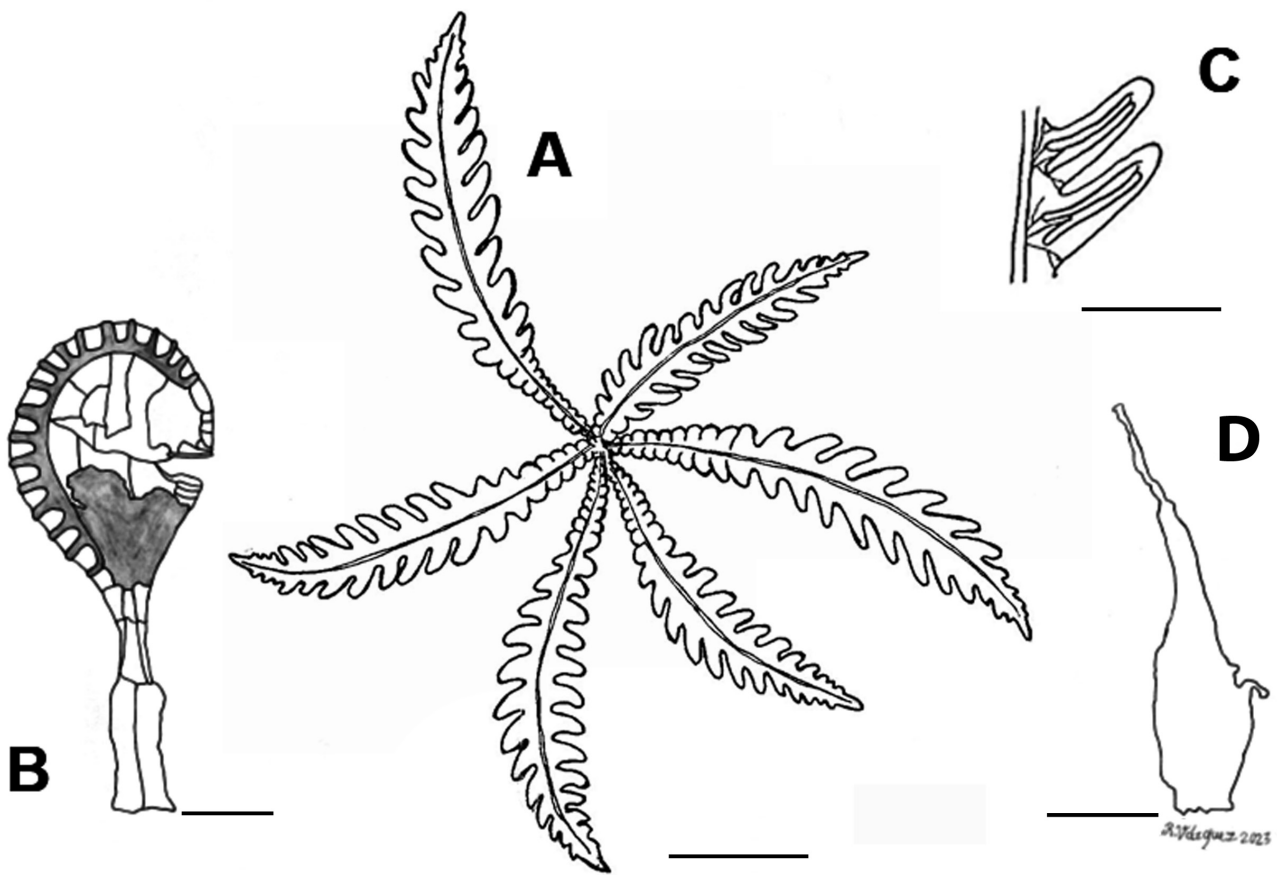


FIGURE 16. Illustration of *Struthiopteris fallax*. A. Habit; B. Sporangium; C. Detail of the sori; C. Rhizome scale. (*P. Wasowicz & J.M. Gabriel y Galán s.n.*, MACB109359). Scale: 1 cm in A; 100 μ m in B; 0.5 cm in C; 500 μ m in D.

This plant is the only endemic fern in Iceland, and its area is estimated to cover only about 100 m² with 100–200 individuals (Löve & Löve 1966, Wasowicz *et al.* 2017a, b, 2021), which makes it a very special element and may be particularly endangered due to the few individuals and the very specific area it occupies.

Material reviewed:—ICELAND. Deildartunguhver, *P. Wasowicz & J.M. Gabriel y Galán s.n.* (MACB109359!).

***Struthiopteris spicant* (L.) Weiss** (Figure 9F; Figure 14E–F; Figure 17).

Type:—SWEDEN. Scania, no date, *no collector* (LINN1244.14! photo, lectotype, designated in Jonsell & Jarvis 1994).

Synonyms:—*Osmunda spicant* L.. *Onoclea spicant* (L.) Hoffmann (1796: 11). *Acrostichum spicant* (L.) Willdenow (1787: 289).

Blechnum spicant (L.) Roth. *Asplenium spicant* (L.) Ehrhart (1788: 95). *Lomaria spicant* (L.) Desva.. *Lonchitis-aspera spicant* (L.) Farwell (1931: 277).

=*Blechnum doodioides* Hooker (1840: 263). Type:—INTERIOR OF N.W. AMERICA. no date, *D. Douglas s.n.*, Herbarium Hookerianum 1867 (K001092778! photo, holotype). *Struthiopteris doodioides* (Hook.) Trevisan (1869: 571).

=*Blechnum heterophyllum* Opiz (1820: 18). Type:—UNITED KINGDOM. Tunbridge Wells, Kent, 1853, *Wollaston s.n.* (not found, synonymy based on the current usage of the name).

=*Acrostichum lineatum* Cavanilles (1799: 106). Type:—CANADA. Nutka, *L. Néé s.n.* (MA228872!, MA228872-2! lectotype, **designated here**; MA475363! isolectotype).

=*Acrostichum nemorale* Lamarck (1779: 11). Type:—FRANCE. no date, *no collector* (not found, synonymy based on the protologue current usage of the name).

=*Lomaria crenata* Presl (1825: 51). Type:—CANADA. Habitat in Nutka, no date, *no collector* (not found, probably at PR, synonymy based on the protologue and current usage of the name); =*Blechnum spicant* (L.) Roth var. *crenatum* (C.Presl) Moore (1857a: 205). *Struthiopteris spicant* (L.) Weiss var. *crenata* (C.Presl) Henry (1915: 3).

=*Lomaria spicant* (L.) Desv. var. *elongata* Hooker (1860: 15). Type:—CANADA. Nutka Sound, no date, *Ihcnke s.n.*; Juan de Fuca, no date, *Brackenridge s.n.*; Observatory Inlet, *Dr. Scolder*; UNITED STATES OF AMERICA. Island of Sitkha, no date, *Eschscholtz s.n.*; Port Etches, Prince William's Sound, no date, *Hinds s.n.* (syntypes, not found, synonymy based on the protologue and current usage of the name). =*Blechnum spicant* (L.) Roth (1794: 56) var. *elongata* (Hook.) Boivin (1967: 649).

=*Lomaria spicant* (L.) Desv. f. *bipinnatum* Clute (1907: 19). Type:—CANADA. Vancouver Island, no date, *no collector* (not found, synonymy based on the protologue and current usage of the name). ≡*Blechnum spicant* (L.) Roth f. *bipinnatum* Clute (1911: 72)
 =*Blechnum spicant* (L.) Roth var. *serratum* Woll in Moore (1857b: 43C). Type:—UNITED KINGDOM. England, Tunbridge Wells, Kent, no date, *Wolaston s.n.* (not found, synonymy based on the protologue and current usage of the name) ≡*Lonchitis-aspera spicant* (L.) Farwell (1931: 277) var. *serrata* (Woll ex T.Moore) Farwell (1931: 277). *Blechnum spicant* (L.) Roth f. *serratum* (Woll ex T.Moore) Broun, (1938: 31). *Lomaria spicant* (L.) Desv. f. *serrata* (Woll ex T.Moore) Clute (1907: 19).
Invalid denominations: *Blechnum spicant* (L.) Withering (1796: 765) nom. inval.; *Blechnum spicant* (L.) Smith (1793: 411) nom. inval.; *Osmunda borealis* Salisburi (1796: 402). nom. sup. *Blechnum boreale* (Salisb.) Swartz (1801: 75). nom. sup. *Lomaria borealis* (Salisb.) Link (1837: 80). nom. sup.; *Blechnum septentrionale* Sailer (1841: 306) nom. inval.; *Spicanta borealis* (Salisb.) Presl (1849: 114). nom. sup.; *Blechnum spicant* (L.) Roth f. *pectinatum* Clute (1911: 73). nom. nud.

Plants terrestrial; *rhizomes* thick, short, covered with linear-lanceolate scales, (0.5) 3–9 x 0.6–0.8 (3.1) mm, discoloured, dark brown, centre narrowly sclerotized from base to apex, margin entire or toothed, lighter brown; *fronds* dimorphic, forming rosette; *sterile fronds* (12) 25 (56) cm, prostrate, *stipes* short, 0.7–5 (17) cm, dark brown, black or atropurpleous, *laminae* narrowly lanceolate to oblong lanceolate, 1.3–7 x 8–65 (100) cm, pinnatipartite or pinnatisect, apex pinnatifid, rarely conform, with uniseriate multicellular hairs ending in a red gland, *rachis* grooved adaxially, green or light brown towards the apex, with glandular hairs like those on the lamina, *pinnae* tapering towards the base, the middle ones 0.2–0.5 x 0.8–6 cm, *veins* free, simple to 1-furcate, catadromous, ending in adaxial submarginal hydathodes, *stomata* aligned following veins on abaxial face of pinnae; *fertile fronds* 36 (75) cm, arising from the central part of the rosette, erect, stipe long, (2) 10–21 cm, dark brown, black or purplish, red in growth, *laminae* lanceolate, 2–4 (8) x 14–54 cm, pinnatipartite or pinnatisect, apex pinnatifid, rarely conform, with uniseriate multicellular hairs ending in a red gland, *rachis* grooved adaxially, green or light brown towards apex, with glandular hairs like those on the lamina, *pinnae* more widely spaced and contracted, the middle ones 0.1–0.2 x 0.7–6 cm; *sori* linear, continuous, forming coenosori on both sides of costa, occupying the entire length of the pinna, decurrent towards the rachis; *indusia* compound, continuous; *sporangia* with 12–18 cells in the arc; *spores* ovoid, 20–35 x 30–50 μm, perispores brown, rugulate, slightly folded.

Habitat and distribution: Europe (from Sweden-Poland-Ukraine-Romania to Iceland), North Africa (where it is rare), the Macaronesian archipelagos (Canary Islands, Madeira and Azores) and the Pacific area of North America (California, Oregon, Washington, Alaska and Canada) (Figure 2). Usually calciferous (Lawalrée 1964), humid and shady areas (Ormonde 1986). Usually grows in forests, meadows, meadows, meadows, rocky ravines, and peat bogs (Rolleri & Prada 2006). From sea level to 3400 m.

Chromosome number:— $n = 68$, tetraploid (Manton *et al.* 1986).

Etymology:—The fertile pinnae give this plant a spiky habit, hence its specific epithet, *spicant*.

Vernacular names and local uses:—Felecha (“arrow”, Bable), sardina (“sardine”, Bable); blècnum (Catalan); žebrovice různolistá (Czech); kambregne (Dannish); deer fern (English); hard-fern (English); herringbone fern (English); orrazi-iratzea (“comb fern”, Euskera); kampsaniainen (“comb fern”, Finnish); dubbelloof (“double foliage”, Flemish); Fougère-en-épi (“Fern-on-the-cob”, French); blechno (Galician); fenta (“fern”, Galician); rippenfarn (“rib fern”, German); erdei bordapáfrány (Hungarian); skollakambur (“devil’s comb”, Icelandic); lonchite minore (“minor lonchite”, Italian); varpotoji unksmenė (Lithuanian); bjønnkam (“comb fern”, Norwegian); Podrzeń żebrowiec (Polish); fetopente (“comb fern”, Portuguese); Дербьянка колосистая (Russian); rebrovka rôznolistá (Slovakian); rebrenjača (Slovenian); lonchite (Spanish); lonquite (Spanish); kambräken (Swedish); Ребрівка звичайна (Ukrainian) (Ormonde 1986, Salvo 1990, Macía *et al.* 2018, Niño Ricoi 2019, iNaturalist 2023, Flora of Iceland 2024). According to a specimen collected by Harlod St. John in Washington, U.S.A. (*H. St. John 4779*, MO1282452), this species is “a favourite of elk”. Quite a few uses have been registered in Spain. For example, in Piloña, Asturias, its occasional use in childbirth has been reported, although it is not specified which part or how it was prepared (San Miguel 2004). It has also been used as a decorative and ornamental plant (Verde *et al.* 2000) and to make floral bouquets together with other ferns (Blanco 1996). Likewise, one of its vernaculars in Bable (Asturian language), “sardina” (sardine), refers to the resemblance of the fronds to a fish scrape, and was used by young girls to play at cooking (San Miguel 2004). Despite this, it is considered a little-used species with very little known data on its use in past times (Macía *et al.* 2018).

Taxonomic notes:—It is common to find individuals with furcate apexes. Indeed, this had led to some authors to describe different forms. Population genetic studies have been conducted both in America (Soltis & Soltis 1988) and northern Europe (Korpelainen & Pietiläinen 2008). In both cases it was saw that populations of this species are genetically very similar, which agrees with later studies that have shown it to be a very young species in geological terms, with a divergence age of half a million years (Molino *et al.* 2019b). However, to our knowledge, there are no phylogeographic studies that include samples from all the centres of diversity of the species (i.e. America, Europe,

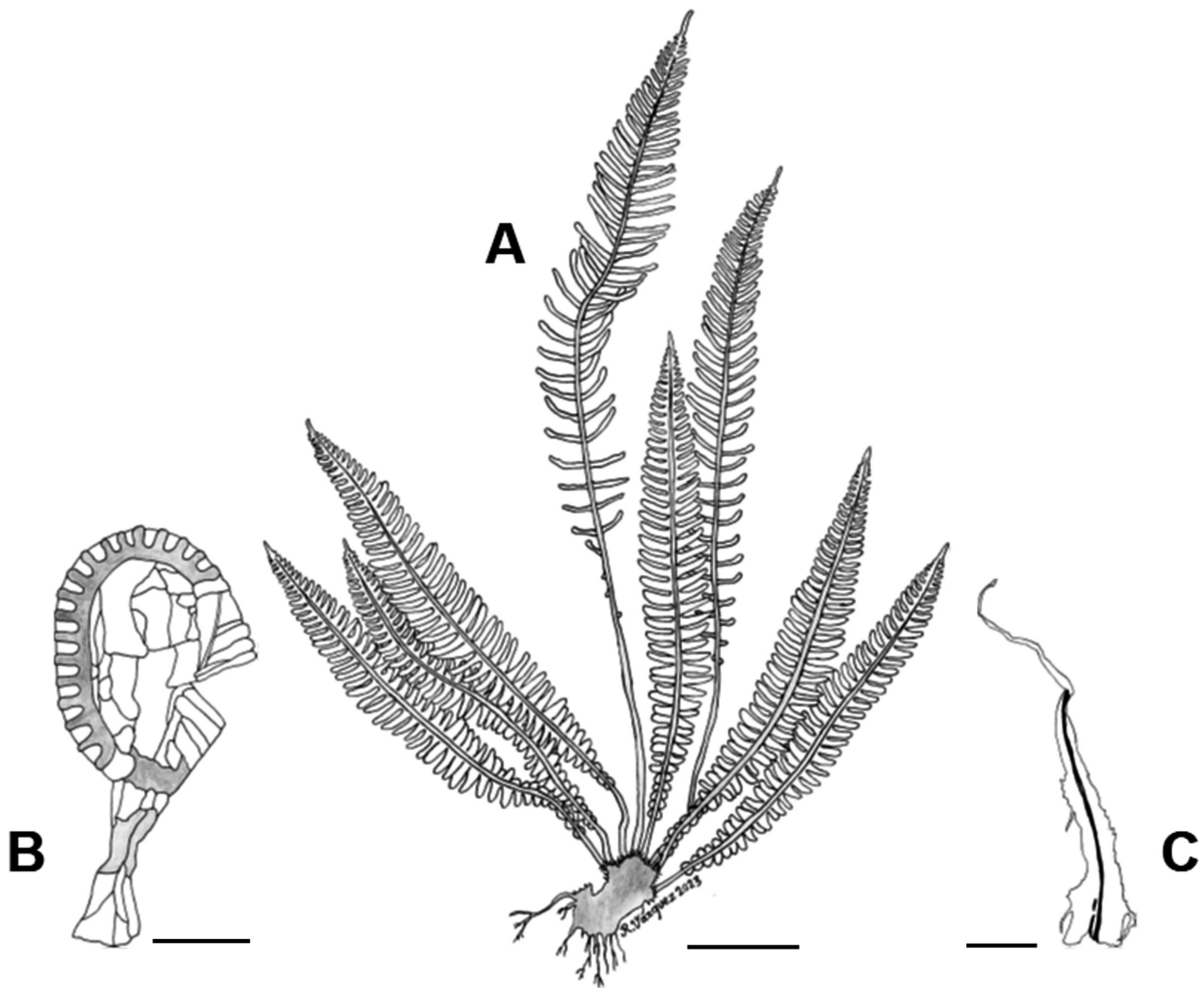


FIGURE 17. Illustration of *Struthiopteris spicant* var. *spicant*. A. Habit (Zollikofer s.n., P01658104); B. Sporangium (J.M. Gabriel y Galán s.n., MACB109622); C. Rhizome scale (*S. Pajarón & E. Pangua* s.n., MACB59142). Scale: 4 cm in A; 100 µm in B; 1 mm in C.

Macaronesia and North Africa). We believe that such a study would be very revealing to clarify concisely the evolutionary history of the species. Apparently, the only morphological differences reported between the American and European plants of *S. spicant* are in size, with the American plants being larger (Löve & Löve 1966). We have not observed this difference in the specimens studied, however it is possible that there is a collection bias, and that the larger specimens have not often been collected because of the difficulty of being pressed. This is why we think that a field study focused on all distribution centres would also be useful to discern the taxonomic status of the American plants with respect to the rest, since they have even been treated at times as distinct subspecies (Löve & Löve 1966). It has also been noted by authors such as Löve & Löve (1966) or Hooker (1840) that phenotypic variation within American plants is lower, and in fact much less variation has been described there than in Europe, where up to twenty-two forms and varieties have been described (Aschenson & Graebner 1912). The study of variation within this taxon carried out by Löve & Löve (1966) concluded that within all these forms and varieties, the only ones that had constant and well-defined characters were *Blechnum spicant* var. *fallax* (now treated as a distinct species) and *Blechnum spicant* var. *homophyllum*. Here we concur with this, adding the variety *pradae*, which was described many years after this study (Molino *et al.* 2019c). To our knowledge, the only variety described in the Pacific populations is *Blechnum spicant* var. *elongata*, named by Hooker (1840) and later discarded by himself (Hooker 1883). A different species was also described from British Columbia, *Blechnum doodioides*, which has turned out to have no real differences with the species *Struthiopteris spicant*.

Additional specimens examined:—**ANDORRA. La Massana:** Arinsal, 5 July 1992, *C. Navarro* CN939 (MA525715!); Arinsal, riu Coma Pedrosa, 2 October 2004, *I. Aizpuru et al.* 10698 (MA720621!). **AUSTRIA. Kärnten:** 14 September 1937, *J.V. Schneider* s.n. (MA894642!). **Niederösterreich:** Höllental, July 1859, *F. Himmelseher* s.n.

(C0379957F!); Krumbach, August 1907, *Krieger s.n.* (MA001476!); *ibidem* (MA001479!); Seitenstetten, 1907, *Strasser s.n.* (MO1877370!). **Tyrol:** no date, *J. Traunsteiner s.n.* (C0379901F!); 1884, *G.C. Jold s.n.* (MO1877383!); Alpes du Stubai, 18 August 1986, *D. Podlech 12898* (MA464909!; P01567060!); Kirchwald, 4–24 July 1977, *M. Pull s.n.* (C0379949F!); Sankt Johan in Tirol, droite d'un sentier montant en direction du Eifersbacherwasserfall et du Angegeralm, August 1989, *G. van Buggenhout 13916* (MA497356!; MO4250370!; P01567062!). **Salzburg:** no date, *no collector 178* (MO1877388!); Hohe Tauern, 20 July 1994, *R.K. Eberwein & E. Vitek 64–193* (C0379940F!; MA767022!); Wald Weslshish, 14 September 1937, *J. Kutshosh s.n.* (P00785357!). **Steiermark:** in silvis vallis Schottelgrabe prope pagum Oberwölz, 1 August 1909, *B. Fest s.n.* (MA001417!). **Vorarlberg:** Bregenz, 6 October 1906, *H. Glück s.n.* (MO972759!); Gósifer Wald bei Feldkirch, 30 October 1876, *H. Klene s.n.* (MA775551!). **Unknown location:** no date, *Poiret s.n.* (P01549459!); no date, *J. Wilde s.n.* (P01417526!). **BELGIUM. Ambers:** bois de hetres et de chênes dénommé "Peerdsbosch", 1 October 1937, *E. Hostié 32* (P01567057!); Turnhout, Engels Kamp park, 18 June 1973, *W. van Cotthem 1123* (MA809713!). **Vlaams-Brabant:** Louvain, 4 October 1903, *illegible collector 6454* (P01549394!). **Wallonie:** Liege, Heppenbach, 9 August 1972, *X. Delannay 4* (MO6604759!); Louette-St. Pierre, July 1860, *Crepin 1922* [interpreted] (C0379959F!). **CANADA. British Columbia:** 3 June 1899, *Wm. Trelease 2705 & A. Saunders* (MO1876819!); Elphinistone Mt., between Sechelt and Gibson, 26 December 1989, *W.H. Lewis & M. Elvin-Lewis 14718* (MO6349329!); Kitlope River watershed, 25 July 1991, *B. Boyle 457* (MO4270239!); Selkirk, 6 July 1905, *C.H. Swaw 835* (MO1876821!); Still water, 15 miles E of Powell River, 9 August 1950, *S. Flowers s.n.* (MO3318339!); Vancouver, August 1890, *H.E. Freeman s.n.* (MO1876845!); Vancouver, 29 July 1909, *J.M. Macoun 84123* (C0602113F!); Vancouver, Kingston, 14 July 1903, *J. Fowler s.n.* (MO828538!); Vancouver Island, 1893, *J. Macoun 41* (MO1876817!); Vancouver Island, District of Renfrew, June–July 1901, *C.O. Rosendahl & C.J. Brand 89* (MO1876818!); Vancouver island, Vicinity of Crofton, 1905, *Mrs. C.E. Young s.n.* (MO840177!); Vancouver island, Vicinity of Ucleulet, 29 July 1909, *J. Maccun 84123* (MO744189!). **CROATIA. Zagreb:** Leskovac, 8 August 1875, *v. de Borbás s.n.* (P01549383!). **CZECH REPUBLIC. Liberec:** am wege von Spindelmühle nach Riesengebirge, 24 July 1889, *C. Felsmann s.n.* (MA001416!); Riesengebirge, Krkonose, 18 August 1888, *A. Poislör 1905* (P01549395!). **Zlín:** Moravia Orient., Valké Karlovice, ad rivulum in valle Milonov in Abieteto, August 1926, *G. Rícan 504* (MO2508748!; MO991327!). **DENMARK.** Faurhult Heat near Frederikshaun, 26 July 1968, *L. Jensen et al.* (MA213361!); Jylland, 17 July 1889, *illegible collector* (MO1877387!); Lys naleskov, Djaulekloften, 16 November 1964, *Munkebjerg 25* (MO3941341!). **FINLAND. Åland:** Sund, 1878, *A. Arrhenius s.n.* (MA001411!). **FRANCE. Alsace:** Ballon d'Alsace (Chaîne des Vosges), 28 July 1959, *B. de Retz 44526* (P01567052!). **Auvergne-Rhône-Alpes:** au pied du Mont Blanc, Haute-Savoie, July 1888, *P. Gave s.n.* (C0379919F!); Blot, no date, *Moufres s.n.* (P01567001!); Cantal, bois de Roquasima à Messillac, près Raulhac, 20 September 1883, *J. de Puyfol 746* (C0379926F!; P01566983!; P01567042!); Chères, 29 August 1887, *V. Auzat s.n.* (P01566988!); France de l'Ouest, Vienne, 28 September 1937, *J. Simon 31* (P01566970!; P01567036!); Isère, Saint-Pierre-d'Allevard, 22 September 1898, *no collector s.n.* (C0379922F!); les bois des montées près Chamonix, no date, *no collector s.n.* (C0379939F!); près Bonneville, Haute-Savoie, 1865, *J. Timothée* (C0379963F!); route D 20F de Roybon à Montrigaud (France, Isère), aux bords du ruisseau qui traverse le premier chemin de chars au début de la descente de la D 20 F vers Montrigaud, 24 Septembre 1971, *R. Barbezat Vidit & A. Lawalrée 5839* (P01567022!); St. Étienne, 1854, *illegible collector 3639* (P01567108!). **Bretagne:** Saint Malo, August 1887 [interpreted], *E. Jeanpert s.n.* (C0379921F!); Serent, Morbihan, environs de La Salle, 31 July 1942, *B. de Retz 18303* (P01567034!). **Centre-Val de Loire:** Loir e Cher, Romorantin, 18 February 1871, *illegible collector s.n.* (P01566979!); Voyer (Cher), 18 October 1901, *illegible collector s.n.* (P01566986!). **Champagne-Ardenne:** Forêt de Cahmpagne, no date, *Devillcers 14* (P01566998!); Villers-Marmery, no date, *M. Remy de Livry s.n.* (P01566966!). **Corse:** Corte, bois humides a la Fontaine de Cadamasse, dans la vallée de la Restonica, 22 July 1932, *B. de Retz 25bis* (P01567051!); Forêt d'Aitone, 13 June 1885, *E. Reverchon 21* (MA001412!; P01549450!); Forêt d'Aitone, Bocca di Vèrghju, Evisa, 18 August 1996, *L. Serra & A. Bort 4865* (MA622949!); Forêt de Vizzavona, Basses pentes au Monte d'Oro, entre le Col et la Cascade des Anglais, 20 July 1954, *B. de Retz 34457* (P01567043!); Ghisoni, forêt dom le de Marmano, 6 January 1899, *R. Rotges 12* (P01566985!). **Franche-Comté:** Champagny, Mont du Chanoi, 1974, *F.-X. Vendrely s.n.* (P01566975!); Champagny, 1889, *illegible collector s.n.* (P01566981!); Ferté, no date, *no collector 1405* (P01566993!); NW de Ronchamp, Champagny, Mourière, 1974, *F.-X. Vendrely s.n.* (P01566994!); Saône, 14 June 1894, *R. Marie s.n.* (P01566999!); Vielle-Hutte, 1974, *F.-X. Vendrely s.n.* (P01566995!). **Grand Est:** Chaîne des Vosges, bords tourbeux du Lac de Lispach, 5 August 1934, *B. Retz 9013* (P01567027!); Flornoy (Haute Marne), Regny-bois, 21 August 1904, *C. Thomas s.n.* (P01567047!); *ibidem*, 1 September 1932, *B. de Retz 2865* (P01567038!); *ibidem*, 8 August 1961, *B. de Retz 48218* (P01567046!); *ibidem*, *B. de Retz 48220* (P01567039!); Le Mussey, 27 June 1874, *illegible collector s.n.* (P01566982!); Le Rothenbachkopf, Chaîne des Vosges, 11 August 1935, *B. de Retz 10489* (P01567026!); Moselle, 12 August 1934, *M.*

de Wailly 4304/4313 (P01567041!); Remiremont (Vosges), September 1844, *A. Tocquaine 1912* (P01549426!); *ibidem*, *A. Tocquaine 194* (C0379906F!; P01566980!); Vosges, 1811, *J.B. Mougeot Bruyériensis M.D. & C. Nestler Argentinensis Pharm 110* (C0379950F!; MO1611160!); *ibidem*, 2 August 1933, *Bois s.n.* (P01566977!); Vosges, 6 October 1937, *B. de Retz 30* (P01567040!); Vosges, massif du faud Ballon, près du rñeservoir de la Lauch en moutaut vers le Marmsteiu, 6 October 1937, *B. de Ritz 30* (P01566974!). **Haust-des-France:** Beauvais (Oise), lande ombragée en lisière du Bois de Belloy, 26 June 1932, *B. de Retz 25ter* (P01567037!); Forêt de Hallotte, Mont Pagnotte, 25 October 1961, *H.E. Jeanpert s.n.* (C0379913F!); Nord, pentes et vallée sud-ouest du Mont-Noir, près de Bailleul, arr. D’Hazebrouck, 9 June 1853, *S.V. Vercier 223* (C0379964F!; P01567000!). **Île-de-France:** Domont, 19 August 1891, *E. Jeanpert s.n.* (C0379923F!); Forêt de Marly, Carrefour des Essants, 11 September 1910, *H.E. Jeanpert s.n.* (C0379936F!); Forêt de Marly, partie de la forêt au S. de la gare de S Nom la Breteche, 22 May 1949, *H. Laurence s.n.* (P01566978!); Forêt de Montmorency, près St. Leu, 9 January 1898, *H.E. Jeanpert s.n.* (C0379937F!); Forêt de Rambouillet, Seine et Oise, bois humides au sud de l’étang d’Angennes, 6 Septembre 1942, *B. de Retz 18473* (P01567035!); Vallen de la Guesle, Poigny, 2 July 1939, *G. Dillemann s.n.* (P01566990!). **Limousin:** Cantal, le long du GR400 entre Aubusson (au-dessus de St Julien de Jordanne) et le Puy Bassiérou, près d’un ruisseau, 11 June 2009, *G. Rouhan & M. Gaudeul 976* (P00577715!). **Loire:** Forêt de Bercé, 1899, *V. Jamin s.n.* (P01660190!); *ibidem*, November 1900, *V. Jamin s.n.* (P01658100!); *ibidem* (P01658103!); *ibidem* (P01660191!); Monte Pierre sur Haute, 14 August 1815, *M. Gandoger s.n.* (MA001419!); *ibidem*, July 1878, *M. Gandoger s.n.* (MO1877367!); Mt. Pilat, July 1843, *Mutel 185* (MA135041!). **Lorena:** Bitche (Moselle), 27 July 1850, *F. Schultz 1903* (P01549414!). **Midi-Pyrénées:** Cauterets (Hautes-Pyrenees), Marcadau (Refuge Wallon), 19 August 1928, *B. de Retz 25* (P01567025!); Cauterets (Hautes-Pyrenees), sous le Lac de Gaube, 12 September 1959, *B. de Retz 44703* (P01567045!). **Nord-Pas-de-Calais:** pentes et vallée sud-ouest du Mont-Noir, près de Bailleul, arr. D’Hazebrouck, 9 June 1853, *S.V. Vercier 223* (P01567109!). **Normandie:** Chanteloup, 3 August 1889, *no collector s.n.* (P01566991!); entre Trouville et Honfleur, September 1875, *no collector s.n.* (P01566969!); Forêt de Cerisy, 1873, *no collector s.n.* (P01658102!); *ibidem*, 26 August 1873, *no collector s.n.* (P01658101!); Forêt d’Eu, Poreau de la Madeleine, 9 August 1924, *M. de Wailly 4313* (P01567048!); Forêt de la Londe (près d’Elbeuf), 13 August 1972, *no collector s.n.* (P01359500!); Manche, à Saint-Hilaire-du-Harcouët, 11 July and 28 August 1854, *Brehier s.n.* (P01566987!); *ibidem*, *Brehier 99* (P01566989!); Marais Vernier, September 1945, *no collector s.n.* (P00917150!); Orne, Saint Bénit, sur le Calcaire, September 1879, *E. Reverchon s.n.* (C0379918F!). **Nouvelle-Aquitaine:** Basses Pyrenées, 6 September 1973, *no collector s.n.* (P01567031!); Basses Pyrenees, dans le Vallon de Laxia, 21 July 1941, *B. de Retz 17222* (P01567033!); Biarritz, 19 July 1859, *Illegible collector* (MO1877389!); Biarritz, 1946, *G. Sag 40* (P00041961!); Bois de Guéret, no date, *no collector s.n.* (P01567028!); Corrèze, Forêt de Gimel, 1854, *S. de Daloz s.n.* [interpreted] (P01566997!); Deux-Sèvres, Forêt de Secondigny, 28 July 1940, *L. Rallet 375* (P01566971!; P01567032!; P01567050!); Forêt de la Braconne, près la Belle Etoile, 24 July 1921, *no collector s.n.* (P01617210!); France de l’Ouest, Vendée, St. Hilaire du Bois, 13 June 1937, *J. Charrier 205* (P01566972!; P01567049!); Gironde, Baigneaux, bois au Sud de Baigneaux, entre Baigneaux et Laurenceae, au N de la route de Martres à Cantois, 4 August 1967 – 19 July 1968, *E. Contré & V.J. Callé 5306* (P01567024!); Vendée, St. Cyr des Gâts, 4 June 1926, *J. Charrier 4510* (P01566973!). **Occitanie:** Alto Garona, Bagneres de Luchon, Forêt de Herran, 7 July 1978, *J.M. Montserrat s.n.* (MA808488!); Aveyron, Cantoin, 17 July 1919, *Caibonal s.n.* (MO2357041!); Aveyron, Aubzac (Revel), 1845–1852, *T. Puel 1454* (P01566996!); Lozère, sommet de la Margeride, 20 September 1941, *E. Licent s.n.* (P00708108!); Saleix, Ariège, 14 September 1981, *L. Villar s.n.* (MA808487!). **Pays de la Picardie:** Forêt de Villers-Cotterêts, 1846, *no collector s.n.* (P01567004!); Forêt de Villers-Cotterêts, 6 July 1894, *H.E. Jeanpert s.n.* (C0379914F!); *ibidem* (C0379917F!); *ibidem* (C0379920F!); Serans (Oise), 22 July 1921, *P. Bosserdet s.n.* (P01001059!). **Pays de la Loire:** Forêt de Blois, 20 October 1861, *S. Mathennet 1921* (C0379968F!); Forêt de Perseigne, 8 August 1879, *no collector s.n.* (P01567003!); La Ferrière, 1879, *J. Hommey s.n.* (P01566984!); Marais de Soesmes, August 1879, *A.R. Franchet s.n.* (C0379930F!); Saône et Loire, La Boulage, no date, *F. Chassignol s.n.* (P01567023!). **Poitou-Charentes:** Essards, 9 July 1896, *E. Jeanpert s.n.* (C0379934F!). **Provence-Alpes-Côte d’Azur:** Sources Forêt de l’Esterel, 01 August 1958, *G. Gavelle s.n.* (MA186653!). **Rhône-Alpes:** Route de Roybon a Montrigaud, aux bourds du ruisseau quitraverse le premier che de chars au debut de descente de la D 20F vers Montrigaud, 24 September 1971, *R. Barbezat s.n.* (MA267596!). **Unknown location:** no date, *no collector s.n.* (P01566962!); no date, *illegible collector s.n.* (P01567030!); 20 June 1869, *no collector s.n.* (P01566963!); July 1871, *Illegible collector* (MO1877381!); 1 November 1882, *H.F. Munroe s.n.* (C0379938F!); 26 July 1896, *H.E. Jeanpert s.n.* (C0379935F!); October 1901, *F.G. Walt 1911* (MO92053!; P01549400!); 11 July 1934, *M. Martínez s.n.* (MA001422!); 1902, *C. Thomas s.n.* (P01567044!); illegible location, 1847, *illegible collector s.n.* (P01566967!); illegible location, June 1870, *illegible collector s.n.* (P01566992!); illegible location, *Hirantz s.n.* [interpreted], 1872 (P01566968!); Bois de la couche près autun [interpreted], 13 June 1842, *no collector s.n.* (P01567029!); Novau-Vallée de la Couche [interpreted], 7 July 1898, *illegible collector 414*

(P01567002!). **GERMANY. Baden-Wurtemberg:** 1906, *J. Müller-Knatz* 16727 (P01549428!); October 1906, *W. Wagner s.n.* (P01549420!); 1926, *A. Lösch s.n.* (C0379952F!); Baden-Baden, 5 October 1899, *A. Kunz* 6357 (P01417532!); Herrenau, 16 August 1892, *Hurritgen & A. Kunz 1902* [interpreted] (P01549413!); Schwarzwald, 5 August 1899, *A. Kunz 1892* (P01549448!). **Bayern:** 8 November 1847, *A.M. Einsele s.n.* (C0379942F!); August 1891, *P. Lydon s.n.* (C0379947F!); 14 September 1899, *illegible collector 1891* (P01549438!); August 1900, *J. Kaulfufs s.n.* (P01549439!); 18 August 1912, *illegible collector* (C0379928F!); 14 October 1916, *illegible collector 5165* (C0379944F!); auf Waldwegen und an Graben am Hulberg bei Fischbach nächst Nürnberg, 6 October 1987, *J. Kaulpup s.n.* (MA001472!); Bodenmais, 11 September 1916, *L. Oberneder 5061* (C0379945F!); Elsass, Weissenburg, 24 August 1895, *Spindler s.n.* (P01549421!); Erlangen, no date, *illegible collector*, (C0379895F!); Feuchte Walber und Nürinberg, 8 aug 1903, *J. Kaulfup s.n.* (MA001473!); Feuchte Waldgräben und Ränder eines Waldbaches beim Hambacher Sauerbrunnen zu Birkenfeld, September 1904, *J. Müller-Knatz & F. Wirtgen 462* (P01571950!); Miescach, 1920, *A. Lösch s.n.* (C0379953F!); Oberbayern, Berchtesgadener Alpen, Watzmannstock, zwischen Herrenroit und Kühroint, Fichtenwald, 10 October 1963, *W. Lippert s.n.* (MA186638!); Oberbayern, Waldrander sudlich von Grabenstatt am Chiemses, 1 August 1902, *H. Stadler 772* (MO1704051!). **Berlin:** Melzergrund, 26 July 1901, *F. Woller s.n.* (MA001423!). **Hamburg:** 29 July 1877, *illegible collector s.n.* (C0379971F!). **Hesse:** Hesse-Nassau, 11 October 1896, *Illegible collector 1900* (P01549412!; P01549417!; P01549418!); *ibidem*, August–September 1899, *J. Müller-Knatz s.n.* (P01417513!); Hasse-Nassau, Taurus, Haidtränthal bei Oberursel, 29 August 1894, *F. Wirtgen 6218* (P01417497!; P01417498!; P01417499!; P01417500!; P01417501!; P01417502!); *ibidem*, 29 August 1897, *F. Wirtgen 6359* (P01417530!); *ibidem*, 12 September 1897, *J. Müller-Knatz 6260* (P01465210!); *ibidem*, 11 October 1897, *J. Müller-Knatz 69* (P01417515!); *ibidem*, 11 September 1897, *J. Müller-Knatz s.n.* (P01417487!); *ibidem* (P01417488!); *ibidem*, 1899, *J. Müller-Knatz s.n.* (P01417473!); *ibidem* (P01417474!); *inidem* (P01417482!); *ibidem* (P01417517!); *ibidem*, *J. Müller-Knatz 232* (P01417475!); *ibidem*, September 1900, *J. Müller-Knatz s.n.* (P01417511!); *ibidem*, *J. Müller-Knatz 6224* (P01417545!); *ibidem*, 28 October 1901, *J. Müller-Knatz s.n.* (MA001478!); *ibidem*, 18 October 1903, *J. Müller-Knatz s.n.* (MA001475!); *ibidem*, 7 October 1906, *J. Müller-Knatz s.n.* (MA001480!); *ibidem*, September 1908, *M. Durieu* [interpreted] 9425 (P01417490!); Frankfurt, 1826, *no collector s.n.* (MO1877378!); Frankfurt, July 1826, *G. Engelmann s.n.* (MO1877376!). **Niedersachsen:** Hameln, no date, *Pflümer s.n.* (MO872983!); Hannover, 1889, *Meyerholz 21029* (P01417476!); *ibidem*, 1891, *C. Luerssen s.n.* (P01417520!); Oldenburg, July 1899, *illegible collector 6219* (P01417503!); *ibidem*, 9 September 1904, *illegible collector 9428* (P01465207!); *ibidem*, 10 September 1904, *illegible collector 9416* (P0141756!); *illegible collector 9423* (P01417507!); *ibidem*, *illegible collector 9433* (P01417529!); *ibidem*, *illegible collector 9434* (P01417540!); Oldenburg, Varel, 21 January 1899, *D. Fr. Müller s.n.* (P01417514!); *ibidem*, July 1899, *D. Fr. Müller 6356* (P01417533!; P01417534!); *ibidem*, *D. Fr. Müller 6360* (P01417538!); Piesberg, near Osnabrück, 6 June 1857, *no collector s.n.* (MO1877372!). **North Rhine-Westphalia:** 9 September 1891, *illegible collector 1883* (P01549435!); 3 October 1891, *illegible collector 1884* (P01549429!); 27 October 1891, *illegible collector 1885* (P01549430!); 21 September 1892, *illegible collector 1882* (P01549434!); 7 August 1893, *illegible collector 1881* (P01549433!); 26 June 1899, *illegible collector 1886* (P01549432!); 13 September 1899, *Illegible collector 1887* (P01549431!); September 1899, *F. Wirtgen 6221* (P01417505!); *ibidem*, *F. Wirtgen 6361* (P01417539!); 8 October 1899, *F. Wirtgen 6358* (P01417531!); 30 September 1898, *W. Sinemkam 1895* [interpreted] (P01549447!); September 1899, *F. Wirtgen 1890* (P01549437!); 27 September 1900, *F. Wirtgen 1946* (P01417495!); August 1904, *F. Wirtgen 9424* (P01417496!); Bergisch, 27 October 1897, *illegible collector 1885b* (P01549346!); *ibidem*, 15 September 1898, *F. Wirtgen 6355* (P01417536!); *ibidem*, 28 September 1898, *F. Wirtgen 6216* (P01417493!); *ibidem*, 3 October 1898, *F. Wirtgen 6240* (P01417479!); *ibidem*, 6 October 1900, *F. Wirtgen 1947* (P01417522!); *ibidem*, *F. Wirtgen 6239* (P01417481!); *ibidem*, 2 September 1903, *F. Wirtgen 9324* (P01417491!); *ibidem*, 23 September 1903, *F. Wirtgen 9373* (P01417492!); Bielefeld, 1859, *H. Wagner s.n.* (C0379898F!); Coesfeld, 22 October 1899, *F. Wirtgen 6220* (P01417504!); Lieggebiet, Bröl, 13 September 1899, *F. Wirtgen s.n.* (P01417537!); *ibidem*, *F. Wirtgen 1948* (P014174914); Rheinsprovinz, 20 August 1900, *C. Luerssen 5548* (P01549381!); *ibidem* *C. Luerssen 5551* (P01549385!); *ibidem*, *C. Luerssen 5553* (P01549382!; P01417525!); *ibidem* *C. Luerssen 5557* (P01549384!). **Rheinland-Pfalz:** July 1982, *BRD s.n.* (MO5496043!); 1860, *Haussbueiht s.n.* [interpreted] (P01417521!); 1897–1899, *F. Wirtgen 69* (P01417519!); 22 August 1899, *C. Luerssen 5332* (P01417512!); 20 August 1900, *C. Luerssen 5548* (P01417523!; P01417524!); 28 August 1900, *C. Luerssen 5575* (P01417510!); Nahe, October 1898, *L. Geisenheyner s.n.* (P01417478!). **Sachsen:** August 1904, *K.W. Krieger s.n.* (C0379956F!); August 1911, *E.R. Missbach s.n.* (C0379954F!); Fichtelberg, 6 August 1900, *C. Haussknecht 1889* (P01549440!); Prope Königstein, September 1908, *W. Krieger s.n.* (C0379946F!); Sächsische schweiz, September 1934, *no collector s.n.* (P00847085!); Sandsteingebirge bei Schöna, August 1906, *R. Missbach s.n.* (MA001481!); Waldrand Str. Schönanbilhl Baldenchofen, 11 September 1985, *R. Bussmann RBM309* (MO6133694!). **Sachsen-Anhalt:** Dresden Dist., “Sächsische Schweis”,

31 August 1873, *C. Luerssen 5479* (C0379933F!); Schellbach, 10 September 1910, *Müller-Knatz* (P01417508!). **Schleswig-Holstein:** September 1898, *J. Lenmier 63* (P01417477!); Kreis Pinneberg, 15 October 1899, *J. Schmidt 32* (P01417518!); *ibidem*, September 1903, *J. Schmidt 9375* (P01417506!); Kreis Pinneberg, an Gräben und Knicks um Tangstedt häufig, September 1902–1903, *J. Schmidt 9* (P01549419!). **Thüringen:** Varel, 21 January 1899, *D. Fr. Miller s.n.* (P01417516!); 31 July 1901, *B. Hergt 6217* (P01417509!); Schmücke [interpreted], 30 June 1890, *Guriegun 1899* [interpreted] (P01549415!; P01549416!). **Unknown location:** no date, *illegible collector* (MO1877377!); no date, *Becukach s.n.* [interpreted] (MO1877380!); no date, *ex. Herb. A.N. Desvaux* (P01549436!); no date, *A. Daenen s.n.* (C0379964F!); no date, *G. Engelmann s.n.* (C0379894F!); *ibidem* (C0379900F!); no date, *F. J. Jung 31* [interpreted] (C0379893F!); no date, *I.A. Lapham 43* (C0379967F!); no date, *W. Gmelin s.n.* (C0379969F!); 10 September 1819, *no collector s.n.* (P01567061!); August 1849, *A.C.V. Schott s.n.* (C0379970F!); July 1858, *E. Stizenberger s.n.* (C0379958F!); 3 October 1860, *L. Gommerfeld 17* (MO909691!); 17 August 1864, *L.J. Wahlstedt s.n.* (C0379903F!); 1866, *Fr. Körnicke 1896* (P01549442!); 1865, *H. Eggert s.n.* (MO1877373!); 1869, *H. Eggert s.n.* (C0379896F!); 26 August 1877, *J. Barth 8298* (P01549392!); 1898, *L. Geisenheyner 20912* (P01549386!); 1898, *L. Geisenheyner 20916* (P01549387!); 20 August 1900, *C. Luerssen 5553* (P01417485!); 24 August 1900, *C. Luerssen 5561* (C0379943F!; P01417486!); 1902, *F. Writgen s.n.* (P01417484!); 28 August 1903, *no collector s.n.* (P01417483!); August 1907, *W. Peschlow 83* (C0379951F!); 10 September 1910, *J. Müller-Knatz 12813* (P01465206!); *ibidem*, *J. Müller-Knatz 12814* (P01465205!); 26 July 1919, *Schcuattarch s.n.* [interpreted] (C0379955F!). **GREECE. Creta:** Distr. Kydonia, Inter Skines et Nea Rumata, 24 July 1973, *K.H. Rechinger 45770* (MO6583303!). **Tesalia:** Mont Pelión, 1906, *R. Marie & M. Petitmengin s.n.* (P01567006!). **ICELAND.** Vestfirðir, 8 July 2016, *J.M. Gabriel y Galán & P. Wasowicz s.n.* (MACB110659!). **IRAN. Juzestan:** Ahvaz, bajo Karum, October 1899, *F.M. de la Escalera s.n.* (MA001420!). **IRELAND. Cork:** Doneraile, 1963, *Mrs J. Bodger s.n.* (MO5462759!). **Kerry:** Iveragh, Caherdaniel, 17 Ju 2016, *S. Molino & M. Pachón s.n.* (MACB109619!). **ITALY. Abruzzo:** Teramo, Ceppo, Monte della Laga, bosque della Morricana, 3 August 2002, *A. Herrero 1958* (MA698559!). **Calabria:** Giaja, 1871–1872, *M. Gandoger 1462* (MO1877369!). **Liguria:** San Romolo, San Remo, 12 November 1900, *C. Bicknell 1910* (P01549402!). **Piamonte:** Stresa, Lago Maggiore, 25 July 1900, *L. Pollini & C. Bicknell 1909* (MA001477!; P01549378!; P01549397!); *ibidem*, 4 September 1906, *B. Boigtiaender-Gebner s.n.* (P01549401!). **Sassari:** Mte de Limbara (Sard. September), 1866, *Marcucci s.n.* (P01549454!). **Sicily:** Castelbuono, no date, *Todaro 1391* (P01549406!); Castelbuono, Mt. Colli, 6 April 1874, *Heidenreich 21122* (P01549376!). **Toscana:** Monte Pisano, July 1862, *no collector s.n.* (C0379966F!). **Trentino-Alto Adigio:** Alpi Apuane, versante nord-orientale del M. Altissimo, September 1946, *A. Frichi 12120* (MO1610874!). **MOROCCO. Unknown location:** in monte Yebel Buhaschen (Yebala), 20 June 1928, *P. Font Quer 442* (MA001410!); *ibidem*, *P. Font Quer s.n.* (MA001421!). **NETHERLANDS. North Brabant:** Moergestel, near Putven, 24 July 1920, *M.R.S. Boetje-van Ruyven s.n.* (C0379907F!). **Overijssel:** Denekamp, 11 August 1916, *M.R.S. Boetje-van Ruyven s.n.* (C0379932F!). **Utrecht:** 28 September 1951, *K.U. Kramer s.n.* (MO1635832!). **NORWAY. Hordaland:** Dalvik, near Bergen, August 1946, *P. Humphreys s.n.* (C0379902F!); **Norland:** Grane, 16 August 1927, *P. Benum s.n.* (P01567058!). **Svalbard:** Spitzberg, 1838, *M. Martins s.n.* (P01549411!). **Vestflod og Telemark:** Notodden, 15 August 2004, *P. Sunding s.n.* (MA747921!). **Unknown location:** no date, *A. Blytt 599* (MO1877384!); no date, *C. Rosenberg s.n.* (MA001413!); illegible location, 19 July 1890, *A. Holms s.n.* (P01539374!). **POLAND. Bielsko:** Brodu ad Kaluaria, 1 November 1925, *J. Trela s.n.* (MO1858732!); Carpati Occidentales, Brody, Distr. Wadowice, 15 September 1938, *J. Trela 306* (MO1659338!); Carpati occidentales, Jaworze, distr. Nowy Sacz, no date, *J. Staszkiwicz & K. Szcepanek 501* (MA267595!; MO1770493!). **Liberec:** Riesengebirge, 17 August 1878, *C. Luerssen 8147* (C0379897F!); Lower Silesian: no date, *no collector s.n.* (MO872984!). **Malopolska:** West Carpathian Mts., Beskid Mazy, Tarnawa Górna near Wadowice, on the foot of Mt. Leskowiec, 21 September 1980, *J. Kornas & A. Medwecka-Kornas 60* (MO2888432!). **Silesian:** Distr. Poreba, 13 August 1956, *N. Ralska s.n.* (MO1711825!); West Carpathian Mts., Beskid Slaski, Stozek near Wisla, 24 September 1975, *G. Halastra & E. Regdos 27* (MO3868056!). **PORTUGAL. Alentejo:** Alto-Alentejo, Serra de S. Mamede, Barreirato, 26 April 1957, *J.V.C. Malato-Beliz et al. 4082* (MA270372!); Alto-Alentejo, Serra de S. Mamede, prox de Alegrete, ribeira de Arromches, Porto de Azenha, 3 April 1957, *J.V.C. Malato-Beliz et al. 4193* (MA269488!); Alto-Alentejo, Serra de S. Mamede, Serra da Selada, junto a estrada dos Galegos, May 1957, *J.V.C. Malato-Beliz et al. 4233* (MA269487!); Alto-Alentejo, Serra de S. Mamede, Portalegre, entre S. Julián e a fronteira, margens da ribeira de Xévora, 3 May 1969, *J.V.C. Malato-Beliz et al. 7207* (MA269483!); Alto-Alentejo, Serra de S. Mamede, Portalegre, S. Julián, Monte Sete, margens do ribeiro da Lamaceira, 4 June 1969, *J.V.C. Malato-Beliz & J.A. Guerra 7233* (MA269482!); Alto-Alentejo, Serra de S. Mamede, estrada de Portalegre para S Mamede, prox. Para o cruzamento para o ponto mais alto, 2 July 1969, *J.A. Guerra & J.V.C. Malato-Beliz 7763* (MA269481!). **Algarve:** Serra de Manelique, ribeira de Piroes, 22 April 1968, *J.V.C. Malato-Beliz 5959* (MA269485!); Serra de Manelique, estrada para Alferce (ca. 15 km de Monchique), 22 April 1968, *J.V.C. Malato-Beliz 5985* (MA269484!); Serra de

Monchique, estrada para a Foia, prox do miradouro, Bicas, 28 June 1978, *J.A. Guerra & J.V.C. Malato-Beliz 14907* (MA269479!); Serra de Monchique, Foia, *J.V.C. Malato-Beliz & J.A. Guerra 14974* (MA269478!); Serra de Monchique, estrada Monchique-Saboia, barranco de Maceira, 20 May 1979, *J.A. Guerra & J.V.C. Malato-Beliz 15941* (MA269477!); Serra de Monchique, barranco de Maceira, afluente de Riba de Perna Negra, 30 May 1979, *J.V.C. Malato-Beliz & J.A. Guerra 16040* (MA269476!); Serra de Monchique, estrada Monchique-Saboia, barranco de Mamira, prox de Cimalhas, 31 May 1979, *J.A. Guerra & J.V.C. Malato-Beliz 16058* (MA269475!). **Azores:** Isal, 19 July 1894, *C.S. Brown 327* (US262512!); Santa Cruz, 29 September 1971, *T.L. Monor 15084* [interpeted] (P01567064!); S. Miguel Island, Furnas, Terra Nostra Park, 17 March 2007, *J.A. Ramos & L.G. Quintanilla LGQ765* (MACB113885!); Terceira, 27 June 1894, *W. Trelease 1166* (US816235!). **Aveiro:** Vale do Vouga, Ribeiro da Calada, August 1943, *P.M. Póvoa dos Reis 908* (MO1637038!). **Centro:** Beira Alta, Serra da Estrela, 1952, *J.V.C. Malato-Beliz s.n.* (MA270374!); Beira Alta, Viseu, Santa Comba-Dao, Chamadouro, ponte de Ouveiro, junto da Barragem, 11 June 1982, *A. Marques 2065* (MA385041!); Beira Litoral, Coimbra, Arganil, Benfeita, Pardieiros, mata de Margaraga, 24 July 1982, *A. Marques s.n.* (MA390255!); entre Oronhe e Travasso, a 2,5 km de Travasso, na estrada Agueda-Aveiro, 2 April 1965, *A. Fernández s.n.* (MA195094!); Viseu, Vouzela, Serra do Caramulo, pr. Carvalhal de Vermilhas, 24 March 2014, *J. Calvo 6394* (MA895113!). **Lisboa:** Serra do Sintra, February 1840, *no collector 303* (P01549452!). **Madeira Island:** 1838 to 1842, *Wilkes Explor. Exped. s.n.* (US92905!); entre S. Vicente e a Encumeada, acima do chao de Louros, 8 June 1957, *J.V.C. Malato Beliz 1531* (MA266380!); ER228 road between Encumeada and S. Vicente, 2 May 1998, *L.G. Quintanilla LGQ685* (MACB113887!; MACB113888!; MACB1138889!; MACB113890!); Funchal, Chemin entre Choupana et Quinta de Vale de Paraíso, 23 July 2007, *G. Rouhan & M. Gaudeul 786* (P00577732!); Levada do Furado, estre o Ribeiro frio e o Santo do Serra, 14 June 1957, *J.V.C. Malato-Beliz 1711* (MA266378!); Levada de Casa do Lombo do Mouro, 28 June 2000, *C. Navarro 3377* (MA654709!); Montado dos Persegueiros, junto ao Ribeiro da Partilha, 13 June 1957, *J.V.C. Malato-Beliz 1647* (MA266379; US2290399!); Paul de Serra, próx. Do Pico da Urze, 10 July 1954, *J.V.C. Malato-Beliz 843* (MA266381!); subida de Queimadas para o pico Ruivo, 3 July 1954, *J.V.C. Malato-Beliz 761* (MA266382!). **Norte:** entre Braga e Porto, nas cercanias do Senhor do Perdao, 28 April 1955, *J.V.C. Malato-Beliz 2256* (MA270373!); Fafe, Lameira, Mouta das Regadas, Carvalhal da Cerdeira, 24 Jjul 1977, *J.V.C. Malato-Beliz & J.A. Guerra 13746* (MA269480!); Fervença-Mondim de Basto, 16 July 1997, *D. Soutinho 740* (MA643519!); Mesao Frio, prox ao rio Teixeira, 22 March 1941, *P. Lopes & G. Pedro s.n.* (MA414816!); Minho, Arcos de Vale de Veg Grosevila, num caminho que liga com a estrada para Mourilhoes e a estrada para Gonte da Barca, 13 July 1944, *C. Fontes & M. Myre 9754* (MA001418!); Minho, Ponte de Lima, lieux ombragés humides près de Rebordões, 4 September 1962, *B.V. Rainha & V.J. Callé 5812* (P01567063!); Minho, Viana do Castelo, Ponte de Lima, Arcos, P.N. de las Lagoas de Bertianos, 7 June 2010, *J.L. Fernández-Alonso et al. JFA29196* (MO6423037!); PNA1-Muas-Vila Real, à entrada do PNAL, margem direita da estrada para Lamas de Olo, 6 July 1997, *D. Soutinho 616* (MA643615!); Porto, arredores, Ermezinde numa bouça, 18 June 1941, *J. Castro s.n.* (MA186642!); Serra de Gerês entre baldas e a Pedra Bela, 10 July 1958, *J.V.C. Malato-Beliz 4416* (MA186640!; MA269486!); Viana do Castelo, Caminha, Serra do Arga, Arga de São João, Alto do Espiñeiro, 7 June 2010, *J.L. Fernández Alonso 29170* (MA821590!); Viana do Castelo, Ponte de Lima, Arcos, P.N. de laos Lagos de Bertianos, 7 June 2010, *J.L. Fernández Alonso 29196* (MA821614!); Vila Nova de Cerveira, Gondarém, entre el Estalagem Boega y el Calvario, 5 June 2010, *A. Quintanar Sánchez 3717* (MA824803!). **Ribatejo:** Santarém, Villa Nova d'Ourem, September 1883, *M. Daveau 1033* (P01549396!; P01549410!; P01549449!). **Unknown location:** no date, *Neé s.n.* (MA233979!); debajo de la venta de Cody, bajando a Laguna, *A.J. Cavanilles s.n.* (MA232868!). **RUMANIA. Transilvania:** 16 August 1877, *J. Barth 8298* (P01549388!); Distr. Făgăraș, 17 July 1930, *E.I. Nyárády 1142* (MO110160!). **SPAIN. Andalucía:** no date, *no collector* (MA226680!); Cádiz, Algeciras, 2 July 1979, *E. Salvo s.n.* (MA235635!); Cadiz, Grazalema, 26 May 1890, *E. Reverchon s.n.* (MA001415!); Cádiz, Jerez, June 1908, *M. Gandoger s.n.* (MO1877368!); Cádiz, Jerez, Sierra de Aljibe, 6 November 1880, *Pérez Lara s.n.* (MA001429!); Huelva, Cortegana, 10 June 1931, *E. Gros s.n.* (MA001434!); *ibidem*, 28 May 1976, *B. Cabezudo Artero 1207/76* (MA208547!); Málaga, Sierra de Yunquera, 8 June 1890, *E. Reverchon 1913* (P01549399!); *ibidem*, *E. Reverchon 479* (C0379914F!; P01549453!). **Aragón:** Huesca, Gistaín, Puerto de la Paz, 15 May 1969, *P. Montserrat Recorder s.n.* (MA808472!); Huesca, Benasque, cerca del hospital, 7 August 1986, *L. Villar & P. Montserrat s.n.* (MA382740!); Huesca, Panticieya, August 1918, *L. Atercito s.n.* (MA135039!); Huesca, Sallent de Gállego, barranco de Espelunciecha, 20 July 1981, *L. Villar s.n.* (MA8008489!); Huesca, Valle de Benasque, July 1873, *Frio Trémols s.n.* (MA001436!); Huesca, Valle de Tena, July 1881, *Zubilla s.n.* (MA001428!). **Asturias:** no date, *no collector s.n.* (MA159349!); Ajuyán, 15 January 1994, *T.E. Díaz González s.n.* (MA540468!); Arrás, no date, *Lagasca s.n.* (MA232663!); Bendición, 1 July 1915, *C. Martínez s.n.* (MA001449!); Cangas de Narcea, de Rebollar a Peranzaes, entre la Peña del Trayecto y el alto de la Gubia del Portillón, 24 September 1990, *R. Gamarra & F. Castilla 542* (MA488315!); Cangas de Narcea, Reserva Biológica de Muniellos, 27 September 1990, *R. Gamarra & F. Castilla 603* (MA488333!); Cangas de Onís, Margolles,

Peruyes, 21 May 1995, *M.C. Fernández Ordóñez s.n.* (MA570737!); Castañedo, 20 September 2017, *S. Molino et al. s.n.* (MACB113877!); Cudillero, Ballota (Santa Marina), 24 August 1996, *T. Campón et al 2778AI* (MA594170!); Gijón, 1927, *Miranda s.n.* (MA001471!); intermediaciones de Gijón, 1 July 1926, *F. Miranda s.n.* (MA001470!); in valle, supra Pajares, 14 July 1892, *A.E. Lomax s.n.* (MA001450!); La Bobia, 20 August 1956, *E. Carreira s.n.* (MA205526!); Ligüeria, Sellón, Piloña, 15 November 2000, *E. San Miguel & A. González Vega ESM95* (MA767385!); Luarca, cerca del mirador, 27 May 1971, *P. Montserrat Recorder s.n.* (MA808483!); Otur, 19 July 2017, *J.M. Gabriel y Galán s.n.* (MACB113876!; MACB113879!; MACB113880!); Oviedo, Sierra del Naranco, 13 November 1981, *C. Aedo Pérez s.n.* (MA621935!); pr. Mazo de Mon, 11 October 2009, *C. Aedo Pérez 17041* (MA796535!); Rozapanera, Rifabar, Espinaredo, Piloña, 23 August 2001, *V. Molina Lobo & E. San Miguel ESM320* (MA767385!); Sierra de la Peral, 19 June 1835, *M.C. Durieu 160* (P01549409!; P01549455!); Valdés, Paladepierre, 22 March 2016, *J.M. Gabriel y Galán s.n.* (MACB109612!); Valdés, Luarca, 12 April 2017 *J.M. Gabriel y Galán s.n.* (MACB109615!); Valles, San Román de Villa, Piloña, 11 August 2001, *E. San Miguel ESM312* (MA768386!). **Canarias:** 1801, 1801, *P.M. Broussonet s.n.* (US2360521!); Tenerife, Anaga, 25 October 1989, *A. Santos s.n.* (MA483040!); *ibidem* (MACB36152!); Tenerife, Anaga, 14 September 2017, *J.M. Gabriel y Galán s.n.* (MACB110658!); Tenerife, Cruz de Taganana, October 1897, *A.C. Cook 1054* (C0355923F!; US537012!; US537013!; US316649!); Tenerife, in apertis humidis jofi la cumbre de Anaga, October 1926, *O. Burchard 308* (C0355922F!); Tenerife, Monte de las Mercedes, sobre el barranco de la Mina, hacia la Peña del Inglés, May 1935, *J. Cuatrecasas s.n.* (MA190831!). **Cantabria:** Ahedo, 28 December 1983, *Prieto et al. s.n.* (MA372712!); Ayuela (Uldias), 9 November 1974, *E. Loriente s.n.* (MA656337!); Camaleño, Cosgaya, 8 October 2016, *J.M. Gabriel y Galán s.n.* (MACB109622!); Castro-Urdiales, carretera de Samano a Guriezo, 15 July 1968, *L.F. Aparicio s.n.* (MA755577!); del monte Carrales cerca de Reinosa, no date, *B. Salcedo 158* (MA232562!); de Yera al Pto. De las Estacas de Trueba, 26 April 1982, *A. Barra s.n.* (MA232253!); Fuente Dé, 11 August 1980, *A. Romero s.n.* (MA503610!); Monte Corona (Comillas), 15 June 1995, *A. Guerra s.n.* (MA656340!); Monte San Juan (Ribamontán al Monte), 10 March 1983, *E. Loriente s.n.* (MA656339!); Ogarrío, *P. Sáinz Gutierrez s.n.* (MA001455!); Pedreña (Marina de Cudeyo), 2 January 1983, *E. Loriente s.n.* (MA656338!); Portillo de la Sía, 18 July 1995, *M. Herrera s.n.* (MA570844!); Reserva de Saja, entre Saja y El Tojo, 3 July 1987, *E. Villanueva 1252* (MA499610!); Reserva del Saja, río Saja, 10 August 1984, *A. Izuzquiza & I. de Aldecoa s.n.* (MA506698!); Saja, Los Tojos, *E. Loriente s.n.* (MA656336!); San Miguel de Aguayo, Santa María de Aguayo, cerca del cruce con la nacional, 22 February 1998, *M. Pardo de Santayana 0359* (MA725198!); Santander, no date, *I. Zubia s.n.* (MA001453!); Santander, Ramales de la Victoria, Ancillo, 19 September 1987, *E. Rodríguez & M. Herrera s.n.* (MA412401!); Santander, Resconorio, Pto. De la Magdalena, 12 September 1987, *C.J. Valle s.n.* (MA412536!); San Vicente de la Barquera, 17 August 1983, *C. Aedo s.n.* (MA621936!); Seña, entrada a la gruta, 20 July 1968, *L.F. Aparicio s.n.* (MA755575!); Vega de Pas, Pandillo, 21 September 1998, *M. Pardo de Santayana & D. Pérez del Molino 0521* (MA725197!); Vega de Pas, Portilla, 2 August 1997, *M. Pardo de Santayana 0116* (MA725199!); Vertiente norte del Pto. De Palombera, 25 April 1982, *A. Barra s.n.* (MA232247!). **Castilla la Mancha:** Albacete, Cañada de los Mojones, junto al Arroyo de la Puerta, Villaverde del Guadalquivir, 1 October 1988, *S. Ríos s.n.* (MA508904!); Ciudad Real, Fuencaliente, umbría de Ventillas Garganta de la Chorrera, 17 June 1998, *R. García Río s.n.* (MA712311!); Ciudad Real, Montes de Toledo, Navas de Estena-Portillo de Cijara (río Estena), 27 August 1988, *D. Sánchez Mata s.n.* (MA483500!); Ciudad Real, Puebla de Don Rodrigo, abedular de Río Frío, 3 November 1991, *C.J. Martín-Blanco & Garrido 1096* (MA615760!); Ciudad Real, San Lorenzo de Calatrava, manadero de Hocedilla, 25 October 2001, *M. Bellet et al. s.n.* (MA721877!); Cuenca, Sierra de Valdemeca, 22 July 1974, *G. López s.n.* (MA226677!); *ibidem* (MA232425!); Cuenca, Valdemoro-Sierra, Hoz Malilla, 1 September 2004, *O. García Cardo OGC-419* (MA744048!); Guadalajara, Cantalojas, valle del Zarzas, barranco de La Laguna, 11 August 1985, *J.M. Cardiel s.n.* (MA502078!); Toledo, Castilla Nova, San Pablo de los Montes, 13 June 1924, *E. Gros s.n.* (MA001427!); Toledo, Nacimiento del Río Estena, 19 June 1986, *N. Marcos 1046MG* (MA343502!). **Castilla y León:** Ávila, Arenas de San Pedro, río Pelayo, March 1987, *F. Gómez 1796* (MA653490!); Ávila, Candeleda, 12 October 1986, *P. Vargas & M. Luceño s.n.* (MA526015!); Ávila, Solana de Ávila, bajando desde la central del Chorro, 12 July 2000, *F. Bajo & R. Álvarez 13100RAD* (MA649430!); Burgos, Espinosa de los Monteros, río Trueba, subiendo al puerto de Las Estacas, 5 June 1988, *A. Izuzquiza & I. de Aldecoa 1455AI* (MA430670!); Burgos, San Millán, 27 September 1975, *E. Fuentes s.n.* (MA806461!); Burgos, Tablada del Rudrón, 28 April 1985, *A. Martín & G. Cela 1003* (MA640526!); Burgos, Valmala, Sierra de la Demanda, barranco de La Genciana, en la umbría del monte Trigaza, 29 June 1994, *J.A. Alexandre 432/94* (MA554685!); León, Aira da Pedra, 20 July 1993, *M. de Godos s.n.* (MA711453!); León, Abelgas, 21 August 1995, *E. Puente & M.J. López Pacheco s.n.* (MA592474!); León, Alto de Pajares, 12 July 1985, *A. Penas s.n.* (MA545816!); León, Burón, Monte Mirva, October 1962, *C.M. Romero s.n.* (MA755576!); León, c. 1.5 km E of Puerto del Pontón, 16 July 1985, *P. Frost-Olsen 7334* (MO6589949!); León, Monte 457 de U.P. de Acebedo, 1 October 1962, *no collector s.n.* (MA205524!); León,

Ponferrada, Pinar de Puebla de Lillo, 15 November 1987, *A. Penas s.n.* (MA412438!); León, Ponferrada, montes Aquilianos, camino de S Pedro a S Adrián, 11 June 1982, *Ibañez & G. Nieto Feliner 565GN* (MA315755!); León, Pto. del Pontón, 23 August 1983, *M.P. Fernández Areces & F.J. Pérez Carro s.n.* (MA318284!); León, Puerto Ventana, 13 August 1979; *J.A. Devesa s.n.* (MA503625!); León, Ravanal de Luna, 30 August 1979, *J.A. Devesa s.n.* (MA503625!); León, S. Teleno, valle del Pelar, 1 July 1946, *F. Bernis Madrazo s.n.* (MA001441!); Salamanca, Bejar, 18 March 1974, *J. Aldasoro s.n.* (MA654364!); Salamanca, Carretera a La Alberca, 14 November 1989, *F.J. González et al s.n.* (MA790486!); Salamanca, carretera de Las Batuecas, la Alberca, 23 June 1946, *A. Caballero s.n.* (MA001451!); *ibidem* (MA001452!); Salamanca, Madroñal, 14 November 1989, *M. Laredo s.n.* (MA570885!); *ibidem* (MA505326!); Salamanca, Navasfrías, 18 July 1976, *E. Rico s.n.* (MA205525!); Salamanca, Pastores, Presa del río Agueda, 19 June 1986, *E. Rico s.n.* (MA390655!); Salamanca, San Miguel de Valero, fuente del Lancharejo, 17 August 2004, *A. Izuzquiza & A. Campón 3363* (MA850548!); Salamanca, Sierra de Francia, June 1904, *M. Gandoger s.n.* (MO1877366!); Segovia, Cerezo de Arriba, La Pinilla, 11 July 1982, *T. Romero s.n.* (MA566192!); Segovia, Pinar del Balsain, 10 June 1889, *Cutanda s.n.* (MA001432!); Segovia, Pr. Hayedo de la Pedrosa, 9 October 2007, *J. Calvo JCI659* (MA773246!); Segovia, puerto de la Quesera, 19 October 1978, *P. Blanco s.n.* (MA450684!); Segovia, puerto de la Quesera, Riaza, 19 November 1984, *C. García Rodríguez s.n.* (MA881298!); Segovia, Sierra de Ayllón, puerto de la Quesera, 26 June 1973, *G. López & E. Valdés s.n.* (MA236403!); *ibidem* (MA844727!); Soria, Covalada, 18 August 1947, *E. Guinea s.n.* (MA718298!); Soria, Covalada, 26 August 1959, *A. Segura Zubizarreta 3954* (MA352947!); Soria, Covalada, sierra de Urbión, cabecera del barranco de la Toreda, 8 August 1992, *J.A. Alejandre 693/92* (MA527293!); Soria, Laguna Negra, 21 July 1962, *A. Segura Zubizarreta 3955* (MA352932!); Soria, Talveila, 22 July 1985, *G. Mateo s.n.* (MA318269!); *ibidem* (MA332552!); Soria, Talveila, 23 July 1987, *G. Mateo s.n.* (MA332552!); Zamora, Aciberos, 23 September 2017, *S. Molino et al. s.n.* (MACB110655!); *ibidem* (MACB113878!); Zamora, Figueruela de Arriba, Flechas, 28 February 1998, *P. Bariego Hernández PB40* (MA796587!); Zamora, Micérecos de Tera, Canal del Molino, 18 June 2010, *C. Perez Morales et al s.n.* (MA895314!); Zamora, Requejo, bosque del Tejedelo, 29 September 2008, *D. Losada DL225* (MA889814!); Zamora, San Martín de Castañeda, río Tera, 20 September 1986, *A. Roa s.n.* (MA510070!); Zamora, Tábara, Monte Las Fuentes, arroyo del Casal, 12 September 1996, *P. Bariego Hernández s.n.* (MA652085!). **Cataluña:** Girona, Camprodon, August 1878, *Bolós s.n.* (MA001430!); Lérida, Portilló de Bossost, 31 July 1994, *L. Sáez s.n.* (MA592754!); Lérida, Valle de Arán, September 1848, *A.C. Costa 188* (MA001435!). **Euskadi:** Álava, Inurrieta, 9 June 1925, *J. Ruiz de Azúa s.n.* (MA001468!); Álava, Lagán, Sierra de Cantabria, 17 August 1973, *P. Montserrat & L. Villar s.n.* (MA317972!); Álava, Landa, 22 December, *J. Ruiz de Azúa s.n.* (MA001484!); *ibidem*, 21 December 1929, *J. Ruiz de Azúa s.n.* (MA001483!); Álava, Monte Gorbea (vertiente S.S.E.), 6 July 1925, *J. Ruiz de Azúa s.n.* (MA001485!); Álava, Monte Gorbea, 17 July 1925, *J. Ruiz de Azúa s.n.* (MA001465!); Álava, Munguia, no date, *J. Ruiz de Azúa s.n.* (MA001466!); *ibidem*, 1 July 1929, *J. Ruiz de Azúa s.n.* (MA001482!); Álava, Santa Engracia, 19 July 1925, *J. Ruiz de Azúa s.n.* (MA001464!); Álava, Ulibarri Ollerros, E Portucho, 10 October 1987, *P.M. Uribe-Echebarria s.n.* (MA415386!); *ibidem* (MACB030899!); Álava, Vitoria-Gasteiz, Montes Altos de Vitoria, fuente de las Neveras, 15 November 2004, *P.M. Uribe-Echebarria VIT75754* (MA753174!); Guipúzcoa, Beasain, 27 June 1926, *J. Ruiz de Azúa s.n.* (MA001459!); Guipúzcoa, cerca de Aya, 21 August 1987, *D. Gómez s.n.* (MA415399!); Guipúzcoa, Escoriaza, 18 June 1925, *J. Ruiz de Azúa s.n.* (MA001467!); Guipúzcoa, Gudamendi, 1 August 1978, *S. García Caballero s.n.* (MA502168!); Guipúzcoa, Irún, Urdanibia, 13 May 1983, *P. Catalán & I. Aizpuru 612.83* (MA343491!); Guipúzcoa, Jazquivel, May 1895, *Gandoger s.n.* (MA001460!); Guipúzcoa, Laurgain, 15 September 1991, *P. Garin s.n.* (MA505223!); Guipúzcoa, Lizarrusti, 21 August 1987, *D. Gómez s.n.* (MA808484!); Guipúzcoa, Salinas de Leniz, 22 December 1925, *J. Ruiz de Azúa s.n.* (MA001474!); Guipúzcoa, San Sebastián, no date, *no collector s.n.* (MA167008!); Guipúzcoa, San Sebastián, junto a las torres de Arbide, 24 October 1995, *P.M. Uribe-Echebarria s.n.* (MA570772!); Guipúzcoa, Vergara, 24 September 1926, *J. Ruiz de Azúa s.n.* (MA001461!); Vizcaya, Aránzazu, 28 July 1951, *E. Guinea 1418* (MA389236!); Vizcaya, Bakio, Mte Jata, 24 July 1989, *J.A. Alejandre 978/89* (C0379911F!; MA484836!); Vizcaya, Bedia, 15 August 1925, *J. Ruiz de Azúa s.n.* (MA001463!); Vizcaya, Carretera de Lequeitio a Ondarroa, 16 August 1947, *E. Guinea 2187* (MA165111!); Vizcaya, Durango, 7 January 1926, *J. Ruiz de Azúa s.n.* (MA001458!); Vizcaya, Galdácano, 22 December 1924, *J. Ruiz de Azúa s.n.* (MA001440!); *ibidem* (MA001469!); Vizcaya, Lemona, 21 August 1925, *J. Ruiz de Azúa s.n.* (MA001462!); Vizcaya, Mte. Jata, 7 April 1989, *J.A. Alejandre 33/89* (MA484835!); Vizcaya, Ochandiano, 4 September 1925, *J. Ruiz de Azúa s.n.* (MA001457!); *ibidem* (MA001486!); Vizcaya, Uberuaga, no date, *I. Zubia s.n.* (MA001438!); *ibidem* (MA001439!). **Extremadura:** Cáceres, Arroyo de Sierra de Valdecaballero, 30 September 1978, *J.L. Pérez Chiscano s.n.* (MA227193!); Cáceres, Baños, no date, *no collector* (MA226679!); Cáceres, Borde de fuente, Cañamero, 26 July 1993, *J.L. Pérez-Chiscano s.n.* (MA531011!); Cáceres, Casas del Miravete, 15 May 1980, *D. Belmonte s.n.* (MA392824!); Cáceres, entre Alcorneo y Valencia de Alcántara, 17 May 1992, *E. Rico s.n.* (MA519388!); Cáceres, entre Descargamaría y Martiago, 8 August

1990, *R. Gamarra & F. Castilla s.n.* (MA488475!); Cáceres, Monfragüe, Ribera del río Tajo, 29 May 1986, *E. Rico s.n.* (MA390982!); Cáceres, Valencia de Alcántara, El Pino de Valencia de Alcántara, 14 November 1987, *M.C. Viera 104/97* (MA503568!); Cáceres, Valencia de Alcántara, Jola, 30 October 1987, *G. Fernández s.n.* (MA503624!).

Galicia: no date, *M. Colmeiro s.n.* (MA232665!); 1897, *Merino s.n.* (MA001443!); A Coruña, A Baña, río de Albariña, 29 December 1996, *L.G. Quintanilla & B. Pias 22* (MA590970!); A Coruña, A Baña, río de Portalexe, 5 July 1997, *L.G. Quintanilla 104* (MA590984!); A Coruña, Abegondo, Robledal del perfil, no date, *H. Villar s.n.* (MA163807!); A Coruña, As Pontes de García Rodríguez, 17 June 1999, *Gil s.n.* (MA649754!); A Coruña, Brañas de Brius, 7 April 1964, no collector (MA824008!); A Coruña, Cariño, Landoy, Río das Mestas, bajo Chan da Capela, 20 June 2017, *R. Fernández Perales et al 21* (MA917905!); A Coruña, Caveiro (Puentedeume), 17 April 1991, *M. Hermida s.n.* (MA745386!); A Coruña, Lousame, río de San Xusto, 26 February 1997, *L. Gómez-Orellana & L.G. Quintanilla 73* (MA591006!; intermediate form between *S. spicant* var. *spicant* and var. *homophyllum*); A Coruña, Monfero, Caveiro, 18 October 1986, *S. González Crespo s.n.* (MA382853!); *ibidem* (MACB031064!); A Coruña, Monfero, Xestoso, a orillas del río Frai Bermui, 10 November 1991, *F.J. Silva-Pando s.n.* (MA505181!); A Coruña, Noya, 21 August 1967, *Casaseca & Álvarez s.n.* (MA185026!); *ibidem* (MA487075!); A Coruña, Playa de Boiro, 26 August 1969, no collector (MA717419!); A Coruña, río Eume-Fuentedeume, 2 August 1968, *Carballal s.n.* (MA478950!); A Coruña, Santa Comba, O Pedroso, Fonte Barreña, 22 June 2017, *R. Fernández Perales et al 142* (MA918020!); A Coruña, Santa Cruz, September 1904, *Bescansa s.n.* (MA150175!); A Coruña, Santiago, 24 August 1967, *F. Bellot Rodríguez s.n.* (MA785146!); *ibidem*, 29 July 1967, no collector (MA824045!); A Coruña, Santiago de Compostela, Cantaleta, 29 July 1967, *Álvarez s.n.* (MA198343!); A Coruña, Santiago de Galicia, en el Paular, en San Ildefonso, 29 July 1782, *A.J. Cavanilles s.n.* (MA232869!); A Coruña, Santiago O. Pino, Arca, río Braudelos, cuenca del Ulla, 9 July 1991, *M.J. Romero s.n.* (MA546613!); A Coruña, Zas, Coto de Muiño, 8 November 1989, *A. Estévez González & M.P. González Hernández s.n.* (MA483063!); Lugo, 24 August 1986, *E. Carreira s.n.* (MA462832!); Lugo, Mouromorto, 27 May 1971, *P. Montserrat Recorder s.n.* (MA808482!); Lugo, Murás, Puente Rioboo, 2 August 1987, *F.J. Silva Pando et al s.n.* (MA412515!); *ibidem* (MACB030875!); Lugo, Riberas de León, 25 July 1956, *E. Carreira s.n.* (MA201118!); Lugo, río Rato, 24 August 1984, *E. Carreira s.n.* (MA391545!); Lugo, Sierra del Caurel, Mercurín, 10 July 1994, *E. Blanco 1182EBC* (MA564805!); Lugo, Villardiaz-Fonsagrada, 8 July 1951, *E. Carreira s.n.* (MA172742!); *ibidem* 7 August 1954, *E. Carreira s.n.* (MA172743!); *ibidem*, 10 July 1957, *E. Carreira s.n.* (MA722139!); Ourense, Barco de Valdeorras, tras de Gandara, 25 July 1987, *C. Prada s.n.* (MA412504!); Ourense, S^a de Santa Marta, Castrelo de Minho, 18 July 1935, *A. Rodríguez s.n.* (MA001442!); Pontevedra, Castro-Loureiro, Ju 1910, *A. Casares Gil s.n.* (MA001444!); *ibidem* (MA001445!); *ibidem* (MA001446!); *ibidem* (MA001448!); Pontevedra, Ermelo, Bueu, 10 October 1969, *S. Castroviejo s.n.* (MA198345!); Pontevedra, estación de Redondela, 4 April 1969, *E. Valdés-Bermejo s.n.* (MA855764!); Huertas de Marin, 8 August 1934, *J. González-Albo s.n.* (MA001456!); Pontevedra Lourizan, 20 April 1960, *A. Rodríguez s.n.* (MA201121!); *ibidem* (MA226674!); *ibidem* (MA226675!); *ibidem* (MA226676!); *ibidem* (MA201121!); *ibidem* (MA226676!); Pontevedra, Lovios, Sta. Eufemia, 6 November 1991, *P. González Hernández & J. Vegas Rodríguez s.n.* (MA505180!); Pontevedra, Marin, 1934, *J. González-albo s.n.* (MA001447!); Pontevedra, Mondariz, 20 May 2016, *J.M. Gabriel y Galán s.n.* (MACB113881!); *ibidem* (MACB113883!); *ibidem* (MACB113884!); Pontevedra, Portela, 27 March 1970, *E. Valdés-Bermejo s.n.* (MA857233!); Pontevedra, San Adrián, 10 October 1970, *Carballal s.n.* (MA313241!); Pontevedra, Monte Aloya, Tuy, 15 July 1993, *S. Pajarón & E. Pangua s.n.* (MA540648!); *ibidem* (MACB59142!); Pontevedra, Redondela, 1 November 1976, *I. Barrera s.n.* (MACB004769!); Pontevedra, Vigo, 26 April 1955, *E. Guinea s.n.* (MA228468!).

La Rioja: Daroca de Rioja, barranco de Cabañas en la umbría de la sierra Moncalvillo, 8 September 1995, *J.A. Alejandro 2585/95* (MA565006!); Puerto Piqueras, 8 August 1978, *F. Amich s.n.* (MA213351!); Rasillo de Carmeros, no date, *Iñiguez s.n.* (MA001431!); Santa Coloma, sierra de Moncalvillo, junto al arroyo en el barranco del Manadero, 14 October 1995, *J.A. Alejandro 2589/95* (MA565007!).

Madrid: Dehesa de Somosierra, 31 May 2017, *J.M. Gabriel y Galán & S. Molino s.n.* (MACB109611!); La Hiruela, abedular de La Dehesa, sobre el Jarama, 18 July 2007, *L.M. Ferrero et al LM4199* (MA772506!); Montejo de la Sierra, El Chaparral, 25 August 1908, *M. Rodríguez & López-Neyra 2273* (MA346270!); *ibidem*, *M. Rodríguez & López-Neyra s.n.* (MA346271!); pista forestal de Peña Cebollera, pr. Somosierra, 26 March 1982, *J.J. González AB2138* (MA232435!); Puerto de Canencia, 12 June 1973, *F. Bellot Rodríguez s.n.* (MA699023!); Peñalara, Sierra de Guadarrama, July 1912, *A. Casares-Gil & F. Beltrán s.n.* (MA001424!); Sierra de Guadarrama, Cercedilla, July 1914, *C. Vicioso Martínez s.n.* (MA001425!); Somosierra, no date, *E. Reyes Prósper s.n.* (MA001426!).

Navarra: August 1876, *J.M. Laurgueta s.n.* (MA001437!); Castillo Nuevo, Leyre, 27 September 1972, *L. Villar & P. Montserrat* (MA808485!); Irati, río Urchuria, 3 September 1993, *E. Rodríguez & M. Herrera s.n.* (MA540678!); Isaba, Belagua, 27 August 1973, *L. Villar s.n.* (MA808486!); Monte Errekerena, Esteribar, 25 September 1989, *J. Loidi s.n.* (MA483527!); Puerto de Echegarate, cercanías del Restaurante Alaska, 1 May 1973, *S. Castroviejo s.n.* (MA226673!);

Roncesvalles, subiendo al Puerto de Ibañeta, 5 August 1973, *E. Fuertes et al. s.n.* (MA792927!); territorio Vestizararensi, 7 August 1876, *J.M. Lacoizqueta s.n.* (MA001454!). **Unknown location:** no date, *no collector* (MA163806!); July 1782, *J.A. Cavanilles s.n.* (MA232867!); Sierra de Fontelome, 9 July 1943, *O. Rodríguez s.n.* (MA346305!). **SWEDEN. Dalarna:** Falun, 16 August 1895, *C. Hammso 19753* [interpreted] (P01549375!). **Norrland:** Jamtland, 18 July 1883, *C. Indebetou s.n.* (MA001414!). **Götaland:** Småland, no date, *N.J. Andersson s.n.* (MA153040!). Skåne, Hörby, Härröd, August 1924, *A. Edv. Gorton s.n.* (MO2482457!); Skåne: Smygehamn, 13 July 1974, *illegible collector* (MO6544346!). **Unknown location:** no date, *no collector* (C0379912F!); no date, *N.J. Andersson s.n.* (MO873120!); *ibidem* (MO873972!); June 1882, *L.J. Wahlstedt s.n.* (C0379904F!); 1885, *illegible collector* (C0379905F!); August 1895, *C.F. Curtiss s.n.* (C0379960F!); August 1902, *A.M. Nordström s.n.* (C0379927F!); 19 November 1907, *A.G. Eliasson 20* (MO1153566!). **SWITZERLAND. Berne:** environs du Col de Jaun, 17 September 1964, *B. de Retz 52491* (P01567055!). **Schwyz:** Mt. Rigi, 1883, *B. Fink Herb. s.n.* (MO1877374!); Unteriberg, no date, *Hoppe 21126* (P01549389!). **Tesino:** Lugano, 21 February 1900, *illegible collector* (P01549379!). **Valais:** Haut-Valais, 26 July 1873, *A. Thielens s.n.* (C0379925F!); Kanton Wallis, zwischen Oberwald und Gletsch im Lärchenwald, August 1903, *F.O. Wolk s.n.* (MO2360824!); la Crettaz sur Salvan Bois mossus, Epicea et Mélèze, 23 September 1950, *C. Oberson 456* (P01567056!). **Unknown location:** no date, *no collector s.n.* (C0379924F!); October 1866, *R. Jalling* [interpreted] (MO873964!); 3 August 1870, *Zollikofer s.n.* (P01658104!); September 1873, *A.J. Skutch s.n.* [interpreted] (C0379908F!); 29 September 1906, *Missbarh s.n.* [interpreted] (P01417528!); 18 July 1960, *Binz 3743* [interpreted] (MO3180251!). **TURKEY. Rize:** 6 km antes de Ikizdere, 28 June 2001, *S. Nisa de Oliveira 715* (MA688910!). **UKRAINE. Chernivtsi:** environs of village Shepit, 12 July 1957, *T.J. Omelczuk s.n.* (MO5788513!). **Leopolis:** Galitzia, Juñ 1873, *Illegible collector* (P01549393!); *ibidem*, 19 July 1873, *Illegible collector* (P01549391!). **Vorokhta settlement hromada:** Ivano-Frankivsk Region, vicinity Vorohta, Goverlyanske forestry, spruce-silver fir forest, 16 July 1957, *T.J. Omelczuk s.n.* (MO5759224!). **UNITED KINGDOM. England:** no date, *J.Y. Braeas* [interpreted] (C0379892F!); 2 September 1903, *L.V. Lester-Garland s.n.* (C0379929F!); 31 July 1931, *no collector* (C0379890F!); Dartmoot, Devon, Becky Falls, 10 June 1924, *D.S. Johnson s.n.* (C0379909F!); Devonshire, 13 July 1924, *R.A. Ware s.n.* (MO1055891!); Hampstead, *M. Lagasca y Segura s.n.* (MA167006!); Hastings, October 1866, *Miss J.E. Wilkins s.n.* (C0379910F!); South Somerset, Seven Wells Wood, 30 July 1968, *J.A. Crabbe et al. 11822* (MA195093!; P01567059!); Surrey, Leith Hill, 1914, *E. Crespigny s.n.* (P01549398!). **Scotland:** Argyll and Bute, Mid Ebudes, Mull, Tobermory, 6 July 1970, *J.A. Crabbe & A.C. Jermy 11837* (MA195091!); Braemar, the Cairnwel, 11 August 1970, *S. Castroviejo s.n.* (MA695159!); east Sussex, Mark Cross parish, Saxonbury Hill, 6 km S of Tunbridge Wells, 20 July 1967, *A.C. Jeremy & J.A. Crabbe 11788* (MA195092!); Granpian Hills, no date, *Redfeld s.n.* (MO1877371!); Isle of Arran, 2 ½ miles southwest of Lochranza, near track, 10 June 1973, *L.J. Tuttle 103* (MO6794402!); Loch Katrine, 26 June 1901, *E.T. Harper s.n.* (C0379961F!); south Somerset, over stowey parish, Seven Wells Wood, 3 km S of Nether Sovey, 30 July 1968, *J.A. Crabbe 11822* (MA195093!). **Wales:** Cafrmarthen, at Bot Fawr Forest, 20 August 1963, *J.P.D.W. Payens 286* (MA477087!); Llangollen, 25 August 1892, *A.E. Lomax s.n.* (MO1877382!); Merionethshire, v.c. 48, Cader Idris, south-west of Dolgellau, July 1961, *R.K. Brummitt 61782* (MA186639!); Pysgodlyn Mawr, Glamorganshire, 7 October 1986, *G. Hutchinson & B.A. Thomas s.n.* (MA477087!). **Unknown location:** October 1847, *M. Howae s.n.* (P01549408!). **UNITED STATES OF AMERICA. Alaska:** 1865–1866, *Western Union Extension Telegraph Exploring Expedition* (C0602102F!); Baranoff Island, 15 June 1899, *Wm. Trelease 2707 & A. Saunders* (MO1876815!); Bluff of Salmon river near bridge, 19 July 1924, *K. Whited 1314* (MO926810!); Chomley, 6 August 1929, *G.B. Rigg 81* (C0602131F!); Cordova, 10 September 1939, *J.H. Steenis 4799* (MO1570445!); Evans island, Port San Juan, 29 September 1948, *W.J. Eyerdam 7268* (MO1590419!; MO5460334!); Hope Island, 1867, *A. Kellogg s.n.* (C0602096F!); Kaasan Bay, 26 July 1901, *C.F. Newcombe 162* (C0602101F!); Kake, Luxuriant forest, 12 September 1928, *Y. Mexia 2313* (MO970428!); Ketchikan area, Higgins Rd., 7 April 1963, *B.J. Neiland 800* (MO3729464!); Kuiu Island, Washington Bay, 1 September 1955, *W.J. Eyerdam 8177* (C0602130F!; MO5791710!); Lawson Bay, 1867, *A. Kelbert 51** (US375667!); McDonald Lake, 15 July 1921, *H.M. Smith s.n.* (US1325588!); McDonald Lake region, 19 July 1905, *J.L. Burcham 21* (US422146!); New Metlakahtla, 4 June 1899, *Wm. Trelease 2706 & A. Saunders* (MO1876816!); Port Althorp, 12 August 1927, *H.C. McMillin s.n.* (US2255439!); Port Ashton, 14 August 1936, *Shulman 54* (MO1967968!); *ibidem*, *Shulman 57* (MO1967967!); Prince of Wales Island, Klawak Lake, 12 September 1915, *E.P. Walker 1004 Mrs. E.P. Walker* (C0602143F!; MO822061!); Prince William Sound, Orca, 24 June 1899, *Wm. Trelease 2708 & A. Saunders* (MO1876813!); *ibidem*, 16 August 1936, *I.L. Norberg s.n.* (US2291321!); Port Etches (Hinchinbrooke Island, Prince William Sound), 27–29 August 1837, *G.W. Barclay 1426* (C0602149F!; US3100237!); Sitka, 13 August 1892, *B.W. Evermann 197* (C0602155F!; MO847389!); Stika and vicinity, July 1891, *W.G. Wright 1613* (MO1876812!); Sitka, Harriman Alaska Expedition, 14–17 June 1899, *F.V. Coville & T.H. Kearney 860* (MO1876814!; US421424!); Stevens Pass, Cascades, 18 August 1893, *J.H. Sandberg & J.B. Leiberg 774* (US275667!);

Thum bay, Knoght island, Prince William Sound, 28 September 1939, *W.J. Wywedam 3388* (MO1190672!); Windham Bay, 10 September 1905 [interpreted], *J.D. Culbertson 4963* (MO1876811!; US666096!); Yakobi Island, 14 July 1915, *E.P. Walker 846 & Mrs. Walker* (C0602119F!; MO822065!; US886881!); *ibidem*, 7 August 1921, *J.P. Anderson 1325* (C0602137F!); Yakobi Island, Bohemia Basin, 13 June 1957, *H.T. Shacklette 3864* (US2416216!). **Arizona:** Graham, South of San Carlos Reservoir, 19 June 1938, *M. Ownbey 1648 & R.P. Ownbey* (C0602074F!). **California:** no date, *S.C. Bagg s.n.* (C0602087F!); 2 November 1905, *H.N. Bolander s.n.* (MO1876841!); 2 April 1950, *P.H. Raven 1539* (MO1735285!); ¼ mi below fork, Waddell Creek, Santa Cruz Co, 14 September 1941, *R.W. Storer 156* (US2256485!); 2 miles SE Mendocino, 17 May 1947, *R.W. Storer 401* (US2256636!); along the E. side of Mitchell Creek Road and about 1.3 mi S of the intersection with Simpson Lane, 21 December 2004, *D. Goldman 2992* (P01625270!); del Norte Co., Smith River, 28 July 1940, *D. Desmareae 21448* (MO1876844!); del Norte Co., Smith River, July 1958, *Bronscob 2* (MO5460329!); Eel River, Humboldt Co., 20 September 1920, *R.K. Beattie 5935* (MO5460330!; US2201149!); Humboldt, 8 July 1888, *V.K. Chesnut 3712* (C0602081F!); Inverness ridge, northwest of Inverness, Marin County, 2 February 1941, *R.F. Hoover 4740* (US2019225!); Little River State Park, 25 August 1957, *D. Branscomb s.n.* (US2422496!); Marin Co., Tomales Bay, 5 November 1933, *J.A. Ewan 8105* (MO1069570!); Mariposa, Mendocino city, 9 August 1901, *no collector s.n.* (US466493!); Mendocino Co., 27 August 1957, *H.N. Bolander 1* (MO5460328!); Mendocino Co., May 1866, *H.N. Bolander 6237* (C0602075F!; MO1876842!; US319019!; US319020!); Mendocino Co., 10 July 1931, *M. Jones 19180* (MO1013609!); near Shelttter Cove, Humboldt Co, 31 July 1869, *A. Kellogg & W.G.W. Halford 1175* (MO1876840!; US324088!); Northern California, Mendocino County, Albion Ridge, July 1909, *J. McMurphy 451* (US610983!); on Baltic Creek, about 30 mi NE of Placerville, 5 July 1901, *W.G. Watkins 12* (US413126!); Pigmy forest, 1 ½ mi NE Albion, Mendocino Co., *R.W. Storer 397* (US2256553!); Sansalito, 24 June 1892, *M.A. Howe s.n.* (US591517!); Santa Cruz Co., 23 June 1881, *M.E. Jones 2232* (P01462469!; US220497!); Santa Cruz Co., August 1888, *L.M. Underwood s.n.* (US644165!); Santa Cruz Co., 17 January 1921, *R.S. Ferris 2107* (MO1876843!); Santa Cruz Co, 2 miles SE of Bonny Doon, Laguna Canyon, 19 December 1965, *G. Ledyard Stebbins 6300* (MO6257789!); Santa Cruz Co., along west fork of Waddell Creek about 5 miles inland from the coast, 16 August 1959, *J.H. Thomas 8068* (US2852893!); Siskiyou Mts. 3 2/10 mi above Smith River (Town) on Rd. Tom High Divide, County del Norte, *C.B. Wolf 4020* (US2201135!); Thompson Ranch, 4 miles north of Crescent City, Del Norte Co, 15 august 1946, *A. Carter 1772* (C0602038F!; MO5460331!; MO1652670!; US2259134!); Van Damme State Park, Mendocino County, 23 December 1957, *D. Branscomb s.n.* (US2257262!); Willow Creek, near Eaverville, 15 July 1931, *M. Jones 29179* (MO1013476!). **Idaho:** Clearwater, 12 miles east of Weippe, 17 April 1930, *H.J. Rust 1156* (US1534579!). **Indiana:** LaPorte, Valley of Trail Creek near the town of Trail Creek, 15 August 1934, *R.M. Tryon 210* (C0602090F!). **Oregon:** no date, *L. Summers s.n.* (US967834!); 1838 to 1842, *Wilkes Explor. Exped. s.n.* (US98664!); 1875, *J. Horwell s.n.* (C0602050F!); 1876, *J. Horwell et al s.n.* (C0602039F!); May 1879, *J. Howell & T.J. Howell* (C0602026F!); *ibidem* (MO1876834!); 30 June 1879, *J. Howell s.n.* (C0602080F!); 13 January 1880, *J. Howell & M.O. Rust 9013* (P01462465!); 4 September 1891, *M. Craig 1007* (MO1876837!); 1871, *E. Hall 680* (C0602062F!; C0602086F!; MO1876832!; P01462461!; US bc1523579!); 15 September 1881, *C.G. Pringle s.n.* (C0602068F!); 30 November 1883, *W.C. Ohlendorf s.n.* (C0602069F!); September 1915, *C.G. Pringle s.n.* (C0602044F!); *ibidem* (P01462460!); *ibidem* (P01462463!); September 1924, *L.F. Henderson 760* (MO918276!); ½ mile east of Scottsburg, 19 March 1942, *R.R. Belton s.n.* (US2467153!); Astoria, 1866, *A. Wood s.n.* (MO873122!); Astoria, Clatsop Co., 31 July to 1 August 1915, *W.W. Eggleston 11452* (US768158!); Benton Co., Mary's Peak, 3 August 1986, *H.N. Moldenke 32073 & A. Moldenke* (MO3674116!); Cascade mountains, 5 October 1886, *J. Howell & T. Howell s.n.* (MO1876835!); *ibidem* (P01462467!); Hillsboro, July 1901, *J.E. Kirkwood s.n.* (US692259!); Clackamas Co., August 1899, *A.D.E. Elmer 1620* (MO1876836!); Clackamas Co., Mount Hood, Government Camp, 9 July 1934, *D.S. Johnson s.n.* (C0602057F!); *ibidem* (MO5460332!); *ibidem*, 31 July 1938, *M. Owabay & R.P. Owabay 1805* (MO1190407!); Coos Bay, 20 August 1911, *H.D. House 4736* (US623071!); Cypress forests of Oregon, no date, *J.G. Lemmon s.n.* (C0602027F!); *ibidem* (US967835!); Grays Harbor Co., about 5 miles south of Lake Quinault, 23 June 1941, *H.T. Rogers 819* (MO1282520!); Lane Co, in coniferous woods across the Siuslaw River from Florence, Twp. 18 S, R. 12 W, 28 August 1949, *A.J. Cronquist 6116* (US2017759!); Lincoln Co, 3 mi N of Florence at junction with Mercer Lake Rd, 25 August 1962, *F.R. Fosberg 43183* (US2675147!); Lincoln Co, along stream, Cape Creek, Perpetua Forest Camp, 29 November 1952, *A.N. Steward s.n.* (US2414117!); Lincoln Co., east of Waldport, 1.3 mi, E of Hwy 101 on Wakonda Beach Rd., Siuslaw Nat. Forest, 22 June 1977, *C. Davidson 6052* (US3586564!); Lincoln Co., Otis Junction, 26 July 1940, *D. Demaree 21415* (MO1876839!); Lincoln Co., Yachats, along the Yachats River, 6 August 1928, *L. Constance s.n.* (MO1876838!); Marion Co., Willamette National Forest, along Forest Service Road 4965, 2 miles E of its intersection with Forest Service Road, 6 miles NE of Detroit, 23 July 1993, *Merello et al 855* (MO4402396!); McMinnville, 1876, *Summers 127* (US834117!); McMinnville, 17 September 1878, *Summers s.n.* (US724007!);

Multnomah, Portland, Willamette Heights, 24 August 1902, *E.P. Sheldon 11262* (C0602051F!); near Summit House, Clackamas Co, 2 September 1897, *F.V. Coville & E.I. Applegate 744* (US381024!); near Willamett slough, May 1879, *J. Howell & T. Howell s.n.* (MO1876833!); Pacific Coast, Foley Springs, 16 July 1903, *M.W. Gorman 1663* (US525681!); Pacific Coast, Western Oregon, August 1880, *T.J. Howell s.n.* (C0602020F!); *ibidem* (C0602032F!); *ibidem* (C0602045F!); *ibidem* (C0602056F!); *ibidem* (C0602416F!); *ibidem* (P01462459!); *ibidem* (P01462462!); *ibidem* (P01462466!); *ibidem* (P01462468!); *ibidem* (US834115!); *ibidem* (US834116!); Pacific Slopes, by mountain rills, 15 September 1881, *C.G. Pringle 2713* (MO1876830! US724005!; US834114!); Portland, June 1890, *J.H. Hicks s.n.* (C0602021F!); Portland, 7 May 1905, *W. Palmer s.n.* (US1488133!); Portland, 10 May 1905, *W. Palmer s.n.* (US1488129!); Portland, 2 June 1905, *W. Palmer s.n.* (US1488132!); Portland, 20 October 1905, *W. Palmer s.n.* (US1488131!); *ibidem* (US1488130!); Still Creek Camp, Mount Hood National Forest, 5 August 1927, *E.L. Evinger s.n.* (US2467167!); Tilamook Valley, 1883, *Summers 11868* (P01462464!); vicinity of Oregon city, 18 June 1905, *M.W. Lyon Jr 79* (US622426!); vicinity of Portland, 10 May 1905, *W. Palmer 1450* (US620278!); vicinity of Portland, 22 June 1905, *M.W. Lyon 94* (US622437!); Willamette Heights, Portland, 24 August 1902, *E.P. Sheldon S11262* (US434884!); Yamhill, 29 June 1893, *W.J. Spillman 214* (C0602063F!). **Washington:** August 1893, *J.H. Sandberg & J.B. Leiberg s.n.* (MO1876829!); 11 May 1934, *O.J. Marie 1110* (MO1086174!); base of Mt. Paddo, 6 August 1885, *W.N. Suksdorf s.n.* (C0602148F!); *ibidem* (MO1876826!) *ibidem* (P01462441!); *ibidem* (P01462448!); *ibidem* (P01462451!); *ibidem* (P01462456!); *ibidem*, *W.N. Suksdorf 830* (P01462449!); Bogachiel River, 4 April 1934, *O.J. Marie 1244* (MO1086214!); Callam Co., along state route 112 just northeast of Pysht, 9 August 1996, *J.S. Miller et al 8711* (MO05050899!); Callam Co., logged area 12 miles W. of Lake Crescent, 23 June 1940, *I.L. Wiggins 9443* (MO1876825!); Chehalis Co., Montesano, August 1919, *J.M. Grant s.n.* (MO862793!); Chehalis Co., near Montesano, 30 June 1898, *A.A. Heller & E.G. Heller 3993* (MO1876827!; US333184!); Clark Co., Camas, June 1927, *D.B. s.n.* (MO941722!); Clallam Co., Olympic Mts., June 1990, *A.D.E. Elmer 2803* (MO1876822!); Clallam Co. Olympic National Forest, Elk Brake, 25 August 1921, *H. St. John 4779* (MO1282452!); Clallam Co., Olympic National Forest, near nature trail, Rain Forest Visitor Center, West Side, 18 June 1966, *D.T. Bell 277* (MO6796407!); Clallam Co., Sequim, August 1915, *J.M. Grant s.n.* (MO787460!); Cumberland, 10 September 1917, *W.H. Meyer s.n.* (C0602088F!); Grays Harbor, Hoquiam, 11 July 1907, *H.C. Cowles 572* (C0602095F!; MO746290!); Grays Harbor Co., Lake Quinault, in vicinity of Willaby Forest Camp, on South Shore Rd., 0.3 mi south of Quinault, 28 June 1970, *S. Gleissman 563 SRG* (MO6885583!); Grays Harbor Co., near Lake Quinault, 10 July 1931, *J.W. Thompson 7324* (MO1010104!); Jefferson, along road to Hoh Rain Forest, off U.S. Route 101 approximately 14 miles south of Forks, 22 August 1969, *R.G. Stolze 1340* (C0602106F!); Jefferson Co., Clearwater trail vicinity Braden Cr., 27 July 1924, *I.C. Otis 1316* (US1316812!); Jefferson Co., on brench, Clearwater trail bet. Braden Vr. And Hoh River, 1 October 1924, *I.C. Otis 1395* (US1316816!); King Co., 20 June–12 July 1898, *T.E. Savage et al. s.n.* (C0602154F!); *ibidem* (MO1876823!); King Co., Brooklyn, 20 June – 12 July 1898, *T.E. Savage et al. s.n.* (C0602142F!); *ibidem* (MO1876824!); Co. King, Skykomish, August 1901, *J.M. Westgate 958* (C0602118F!); King Co., Snoqualmie Pass, 17 September 1932, *J.W. Thompson 8928* (MO1030988!); King Co., Seattle, September 1888, *C.V. Piper 10007* (C0602125F!); *ibidem*, September 1892, *E.A. Shumway s.n.* (MO1876728!); *ibidem*, 1 July 1915, *G.W. Freiberg* (MO813660!); King Co., Skykomish, August 1901, *J.M. Westgate 903* (C0602112F!); *ibidem*, August 1901, *J.M. Westgate 935* (C0602124F!); Kittitas Co., Easton, 15 July 1930, *E.J. Palmer 37900* (MO1003177!); Klickitat Co., Bingen, August 1907, *W.N. Suksdorf s.n.* (P01462453!); *ibidem* (P01462454!); Klickitat County, Falcon valley, July 1908, *W.N. Suksdorf s.n.* (C0602094F!); *ibidem* (P01462447!); Klickitat, Mount Binger, 30 June 1908, *W.N. Suksdorf s.n.* (C0602101F!); Olympia, October 1905, *E.C. Townsend s.n.* (MO1214041!); Olympic Peninsula, 15 June 1973, *L.H. Potter s.n.* (MO3101388!); Pierce Co., Puyallup, 17 July 1880, *G. Engelmann s.n.* (MO1876820!); Quiniault, Jefferson, Chehalis and Thurston Co. Granville, 8 June 1902, *H.S. Conard 345* (US526740!); Seattle, August 1898, *C.V. Piper s.n.* (US102542!); Skamania County, 12 August 1899, *J.B. Flett 921* (P01462450!); Seattle, 15 October 1910, *E.M. Bandell & J.C. Frye s.n.* (P01462444!); Snohomish Co, Lee Forest, 0.50 of a mile east of State Highway 1A, approximately 4 miles north of Woodinville, 23 April 1963, *D.R. Simpson 61* (C0602136F!); Snohomish Co., Maryville, August 1924, *J.M. Grant s.n.* (MO922716!); Snohomish Co., Mt. Baker/Snoqualmie National Forest, FR 20, 1 mi N of Barlow Pass, 26 September 1998, *A. Colwell & P. Reeves 142* (MO04895651!); Snohomish Co., trail up Perry Creek, ca. 30 miles east of Granite Falls, Mt. Baker National Forest, 22 August 1969, *J.D. Montgomery 85030j* (MO5460333!); Stevens Pass, Cascade, 18 August 1892, *J.H. Sandberg & J.B. Leiberg 774* (P01462438!); Tacoma, 19 September 1902, *J.B. Flett 2030* (P01462452!); Thurston Co., moist coniferous woods near the head of Mud Bay, about five miles west of Olympia, 15 August 1936, *F.G. Meyer 792* (MO1313447!); Tummel city [interpreted], August 1893, *J.H. Sandberg & J.B. Leiberg s.n.* (P01462442!); Whatcom Co., below Mt. Baker Lodge, N. Fork Nooksack, 24 July 1930, *L. Benson 2367* (MO989086!); Whatcom Co., Mount Baker area, 9 September 1945, *P.O. Schallert 5249* (C0602089F!; C0602107F!); Whatcom Co. Timbered

slopes below Welcome Pass, Mt. Baker region, 20 August 1931, *J.W. Thompson 8057* (MO1009241!). **Unknown location:** 1872, *Hoppe s.n.* (P01549390!); April 1883, *G.E. Davenport s.n.* (P01462458!). **EUROPE (unknown location).** No date, *no collector* (P01549451!); *ibidem* (MO1877!390!); *ibidem* (MO1877391!); *ibidem* (MO1877392!); *ibidem* (MO937727!); no date, *illegible collector* (MO1877386!); no date, *Kühlewein s.n.* (C0379941F!); no date, *Scott 600* [interpreted] (MO1877385!); 1864, *illegible collector* (MO872277!); 1895, *no collector s.n.* (C0379931F!); no date, *Hoppe 1823* (P01417527!); no date, *H. Wagner s.n.* (C0379899F!); 1838, *Martubs 223* (P01549405!); June 1846, *illegible collector s.n.* (P01549377!); 16 July 1889, *illegible collector 16334* (P01549380!); no date, *Ex Herb. Danty d'Insard* (P01549403!).

Struthiopteris spicant (L.) Weiss var. *homophyllum* (Merino, 1898: 108) Gabriel y Galán & Pino in Wasowicz *et al.* (2017b: 198). (Figure 9G; Figure 14G; Figure 18A).

Type:—SPAIN. Galicia, Fig 1c. *Homophyllum blechniforme* in Merino (1898: Lám I), lectotype, designated in Wasowicz *et al.* (2017a).

Synonyms:—*Homophyllum blechniforme* Merino. *Blechnum spicant* (L.) Roth var. *homophyllum* (Merino) Merino (1909: 488).

Blechnum homophyllum (Merino) Sampaio (1934: 66).

Invalid designations: *Blechnum spicant* var. (*sine nomine*) Christ (1917: 8).

Plants terrestrial, *rhizomes* short, covered with triangular-lanceolate, concolorous, brownish-clear scales, without sclerosed centre or slightly sclerosed, (0.5) 3–5 x (0.4) 1–5 mm; *fronds* (6) 12 (22) cm, subdimorphic, rosette-arranged, *sterile* and *fertile fronds* about the same size, shortly petiolate, *stipes* dark brown, black or purplish, 0.3–3 cm, *laminae* lanceolate, pinnatifid or pinnatisect, 0.8–3 x 5–17 cm, apex pinnatifid, rarely conform, with uniseriate, multicellular hairs, topped by a red gland, *rachis* green or brown towards apex, with glandular hairs like those on the lamina, *pinnae* tapering towards the base, the middle ones 0.1–0.4 x 0.6–2 cm, slightly contracted on fertile fronds (0.1–0.3 cm); *veins* free, simple to 1-furcate, catadromous, ending in adaxial submarginal hydathodes, *stomata* aligned following veins on abaxial face of pinnae; *sori* linear on both sides of costa, fragmented, decurrent towards rachis; *indusia* complex, fragmented; *sporangia* with 12–18 cells in arc; *spores* monoletic, 20–40 x 30–50 µm, perispores brown, rugate.

Habitat and distribution:—Northwest and west of the Iberian Peninsula, Pontevedra, La Coruña, Orense, Salamanca, Segovia, Salamanca, and Álava (Spain) and Minho (Portugal) and the Macaronesian archipelagos of Azores (San Miguel) and Madeira (Figure 2). Moist, shady slopes, usually disturbed, almost always in southwestern orientation. Sea level to 500 m.

Chromosome number:— $n = 68$, tetraploid (Löve & Löve 1968, Horjales *et al.* 1990).

Etymology:—The term *homophyllum* refers to the subdimorphic condition of this taxon.

Taxonomic notes:—This variety can be distinguished from *S. spicant* var. *spicant* by its smaller size (20 cm or less) and subdimorphic fronds, with more triangular pinnae and discontinuous sori. It differs from *S. spicant* var. *pradae* also in size, as the *pradae* variety is similar in size to the type variety. In addition, in the variety *pradae* there are sporophylls with the same appearance as the trophophylls, without subdimorphism, which coexist with dimorphic contracted sporophylls typical of the type variety, a feature that does not occur in the variety *homophyllum*. Löve & Löve (1966) cultivated some Spanish specimens and reported that, surprisingly, they maintained their characteristics in culture. However, these same authors report that, contrary to what happens with *S. fallax*, this variety intermingles a lot with the *spicant* variety, appearing many intermediate forms. We have corroborated on the field that there are a lot of transitional forms between *S. spicant* var. *homophyllum* and the type variety with viable spores, one of the reasons why this variety is not elevated to species status.

The original distribution of this variety was restricted to South of Galicia in Spain and north of Portugal. However, this distribution was extended to Salamanca (Molino *et al.* 2019a) and latter on to Azores and Madeira (Molino *et al.* 2021). In this last work it is noted that the Macaronesian individuals were found in habitats with low nutrient viability, which is consistent with the hypothesis of the positive association between leaf dimorphism and resource-rich habitats (Britton & Watkins 2016).

Also, these recent distribution extensions point out that probably *S. spicant* var. *homophyllum* has a more widely distribution than previously thought, and it would be interesting to look for it in more locations, paying special attention to the species' range edge, where this variety seems to be more abundant (Molino *et al.* 2021).

The type, which must be a specimen collected by Merino in San Juan de Tabagón (Galicia, Spain) was not found, so Wasowicz *et al.* (2017a) designated the illustration presented in the original description (Merino 1898, Plate I) as lectotype. Here we have found specimens from La Guardia collected by Merino in 1898 (MA152390!, MA170055!), a locality also mentioned in the species description, and hence we consider them here as original material, however the term “paralectotype” is not usually used on Botany.

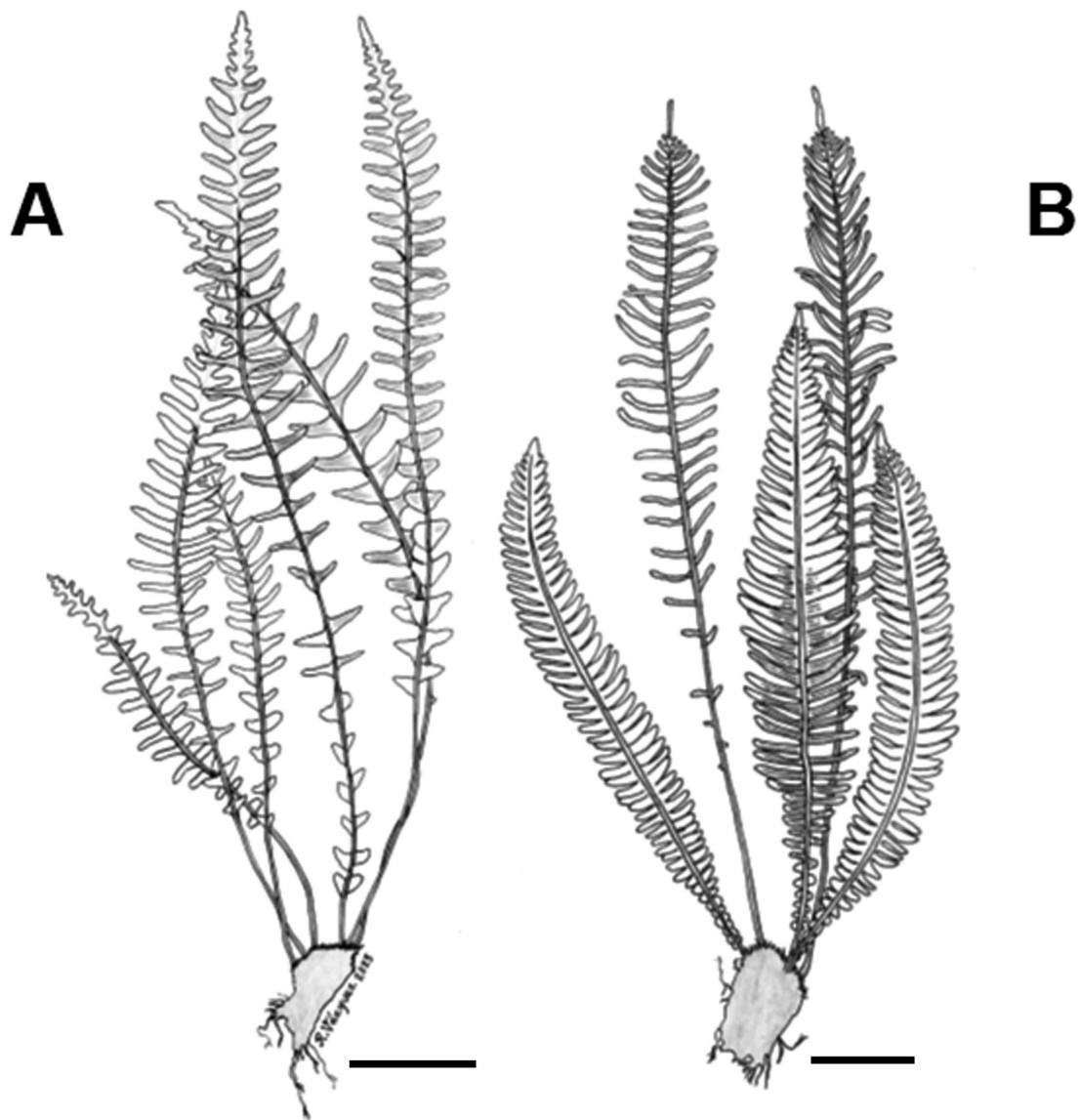


FIGURE 18. A. Illustration of *Struthiopteris spicant* var. *homophyllum* (J.M. Gabriel y Galán s.n., MACB109617); B. Illustration of *Struthiopteris spicant* var. *pradae* (S. Molino et al. s.n., MACB110654, holotype). Scale: 2 cm in A; 4 cm in B.

In Wasowicz *et al.* (2017), the basionym for this variety is said to be *Blechnum spicant* var. *homophyllum* Merino in Christ (1904: 79). However, Merino first described the species within a new genus, naming it *Homophyllum blechniforme* Merino (1898: 108). Later, Merino himself consulted with H. Christ on the status of the taxon and decided to combine it as a variety of *S. spicant* (sub. *Blechnum spicant*), which he published acknowledging Merino (Christ 1904). However, we consider that *Homophyllum blechniforme* was a correctly published name, and there is no reason not to consider it the basionym of the taxon as it was the first one published.

Additional specimens examined:—**PORTUGAL. Azores:** San Miguel Island, Algarvia, 17 March 2007, J.A. Ramos & L.G. Quintanilla LGQ763 (MA939454!); Trilhos Novos, J.A. Ramos & L.G. Quintanilla LGQ764 16 March 2007, (MA939453!). **Madeira Island:** ER228 road between Encumeada and S. Vicente, 02 May 1998, L.G. Quintanilla LGQ682 (MA939455!). **Norte:** Braga, Vieira do Minho, 1 October 2004, C. Prada s.n. (MACB109621!); Minho, Pinheiro, N103 Braga-Chaves rd., 13 July 1974, E.A. Leadlay & B. Petty 392 (MO2358910!); Ponte do Lima, Anais, Fujaens, 9 September 1963, G. Costa s.n. (MA633695!); S. Gregorio do Minho, 14 July 1945, J.G. García 757 (MA270375!). **SPAIN. Euskadi:** Álava, no date, no collector s.n. (MA226678!). **Castilla y León:** Salamanca, Batuecas, 15 May 2016, J.M. Gabriel y Galán s.n. (MACB109626!); Segovia, Valle del Tejadilla, no date, E. Reyes Prósper s.n. (MA001433!). **Galicia:** no date, M. Colmeiro s.n. (MA232665!); A Coruña, A Baña, San Mamede de Monte church, 13 August 2004, L.G. Quintanilla LGQ726 (MA939457!); A Coruña, Mariaqueira river, 21 February 2001, L.G. Quintanilla LGQ777 (MA939456!); A Coruña, Santiago, Cantaleta, 29 July 1967, I.

Barrera s.n. (MACB32367!); Orense, Lovios, Parque Natural do Xurés río Caldo, 4 September 1997, *I. Pulgar & L.G. Quintanilla s.n.* (MA595201!); Pontevedra, Bueu, Ermelo, 11 October 1979, *S. Castroviejo s.n.* (MA198344!); Pontevedra, between Tabagón and Tomiño, 19 March 2016, *J.M. Gabriel y Galán s.n.* (MACB109617!); Pontevedra, La Guardia, *B.P. Merino s.n.* (MA152390!, paratype); *ibidem* (MA170055!, paratype); Pontevedra, Mondariz, 20 March 2016, *J.M. Gabriel y Galán s.n.* (MACB109618!); Pontevedra, Mointe Aloia, regato do Seixal, 31 August 1996, *B. Pias & L.G. Quintanilla 23* (MA591004!).

***Struthiopteris spicant* (L.) Weiss var. *pradae* S.Molino & Gabriel y Galán in Molino *et al.* (2019b: 266) (Figure 9H; Figure 14H; Figure 18B).**

Type:—SPAIN. Zamora, Aciberos, c. 3km west of the village, 42.038942°, -6.861643°, on a shady slope near the road, under *Fraxinus angustifolia* and *Quercus pyrenaica*, 1,220 m, 20 September 2017, *Molino, et al. s.n.* (MACB110654!, holotype).

Plants terrestrial: *rhizomes* thick, short, covered with linear-lanceolate scales, 0.45–1.6 x 4.5–9.5 mm, discoloured, centre sclerotized from base to apex, dark brown, margin light brown, entire; *fronds* dimorphic, forming a rosette; *sterile fronds* (14) 34 (70) cm, *stipes* short, 0.5–6 (18) cm, dark brown, black or purplish, *laminae* narrowly lanceolate to oblong lanceolate, 1.5–6 x 13–30 (56) cm, pinnatifid or pinnatisect, apex pinnatifid, rarely conform, with uniseriate multicellular hairs ending in a red gland, *rachis* grooved on adaxial side, green or light brown towards apex, with glandular hairs like those on the lamina, *pinnae* tapering towards the base, the middle ones 0.2–0.6 x 0.8–3 cm, *veins* free, simple to 1-furcate, catadromous, ending in adaxial submarginal hydathodes, *stomata* aligned following veins on abaxial face of pinnae; *fertile fronds* of two types, both with glandular hairs like those on the sterile fronds, first type (25) 53 (90) cm, arising from the central part of the rosette, erect, *stipes* long, 4–15 (28) cm, dark brown, black or purplish, red in growth, *laminae* lanceolate, 2–6 x 20–40 (63) cm, pinnatifid or pinnatisect, pinnae more widely spaced and contracted, the middle ones 0.1–0.3 x 2–3 cm; *sori* linear, continuous, forming coenosori on both sides of costa, decurrent towards rachis; *indusia* continuous; second type of *fertile fronds* normally a single frond, same aspect as sterile ones but with *sori* in the middle part of the lamina, linear, fragmented on both sides of the costa; *indusia* linear, fragmented; *sporangia* with 13–20 arc cells; *spores* monoletic, 20–40 x 30–60 µm, perispores brown, rugate.

Habitat and distribution:—Known from Northern half of the Iberian Peninsula (provinces of Zamora, Asturias, Burgos, León, and Madrid), Germany (States of Baden-Wurtemberg, Hesse, Niedersachsen, Nordrhein-Westfalen, Rhineland-Bergisch, Rhineland-Palatin and Schleswig-Holstein) and sparse collections of Alsace (France), Steiermark (Austria) and Scotland (Figure 2). Probably more abundant. Moist slopes.

Chromosome number:—Unknown.

Etymology:—This variety is dedicated to the reputed Spanish pteridologist Carmen Prada, who has devoted much of her life to the study of ferns, being a teacher, inspiration and mirror of good work for several generations of pteridologists and botany students.

Taxonomic notes:—The detection of several specimens of this variety in herbarium specimens from Germany led us to suspect that these phenotypic variations had been studied in the past. Indeed, we found two 19th century works describing several varieties within the species (Luerssen 1889, Wilhelm & Laubenburg 1897). Among these varieties, the one described as variety *complexa* seems to be similar to variety *pradae*. In particular, intermediate fronds are described, with trophophyllous appearance but with fragmented sori in the middle zone of the frond. However, we have found no evidence in either work to confirm that in these specimens intermediate fronds coexist with normal dimorphic sporophylls, a feature that is fundamental according to the original description of *S. spicant* var. *pradae* (Molino *et al.* 2019c). Similarly, high importance is given in both Luerssen (1889) and Wilhelm & Laubenburg (1897) work to the relative length of the stipe, a trait that proved not to be significant in differentiating the different varieties (Molino *et al.* 2019bc).

Likewise, in the sheet review we have carried out, we have seen that the extent of the variety *pradae* is much greater than previously reported, as had already begun to be noted in other studies (Molino *et al.* 2021). *Struthiopteris spicant* var. *pradae* is not, therefore, an Iberian endemism, but extends at least as far as Austria, France, Scotland, and Germany and could probably be even more widespread.

Additional specimens examined:—AUSTRIA. **Steiermark:** Waldbach, August 1904, *F. Wirtgen 9440* (P01465181!). FRANCE. **Alsace:** Hagenau, June 1834, *Grenier s.n.* (P01566964!; P01566965!). GERMANY. **Baden-Wurtemberg:** Baden-Baden, 5 October 1899, *A. Kunz 6285* (P01465178!). **Hesse:** 2 September 1899, *F. Wirtgen 6283* (P01465185!); Taurus, Heidtränkskal, 29 August 1897, *F. Wirtgen 6264* (P01465204!); *ibidem*, *F. Wirtgen 6288* (P01465179!; P01465180!); *ibidem*, September 1900, *J. Müller-Knatz 6298* (P01465193!); *ibidem*, *J. Müller-Knatz 6303* (P01465195!). **Niedersachsen:** Oldenburg, 10 October 1904, *illegible collector 9439* (P01465203!). **Nordrhein-**

Westfalen: 9 October 1900, *Wirtgen 6295* (P01465191!); 5 July 1901, *F. Wirtgen 1849* (P01465194!); *ibidem*, *F. Wirtgen 1850* (P01465198!); *ibidem*, *F. Wirtgen 1852* (P01465175!); *ibidem*, *F. Wirtgen 1853* (P01465176!); 6 July 1901, *F. Wirtgen 1854* (P01465177!); Bröl, 13 September 1899, *F. Wirtgen 6297* (P01465190!); Rüdighausen, 6 July 1906, *F. Wirtgen 1855* (P01465209!). **Rhineland-Bergisch:** Bergisch, 27 October 1897, *F. Wirtgen 6286* (P01465187!); *ibidem*, 3 October 1898, *F. Wirtgen 6287* (P01465186!); *ibidem*, 30 August 1900, *F. Wirtgen 6282* (P01465183!; P01465184!); *ibidem* (P01465188!); *ibidem*, 15 September 1900, *F. Wirtgen 6299* (P01465196!); *ibidem*, September 1900, *J. Müller-Knatz 6300* (P01465197!). **Rhineland-Palatinate:** Gerolstein, 25 August 1899, *Wessam* [interpreted] 6284 (P01465182!); Krautscheid, 1901, *F. Wirtgen s.n.* (P01465173!); *ibidem* (P01465174!). **Schleswig-Holstein:** Kreis Pinneberg, September 1902–1903, *Schmidt 9329* (P01465208!); *ibidem*, September 1905, *Misbanth 11716* (P01465201!). **Unknown location:** 9 November 1902, *Alf. Hirth s.n.* (C0379948F!); 1906, *illegible collector 12773* (P01465200!); 1906, *illegible collector 12777* (P01465189!); August 1906, *illegible collector 12772* (P01465201!); *ibidem*, *illegible collector 12779* (P01465199!). **SPAIN. Asturias:** Valdés, Paladeperre, 22 March 2016, *J.M. Gabriel y Galán s.n.* (MACB109613!); *Ibidem*, 3 August 2016, *J.M. Gabriel y Galán s.n.* (MACB109615!); Luarca, 26 July 2017, *J.M. Gabriel y Galán s.n.* (MACB110660); Otur, 17 August 2017, *J.M. Gabriel y Galán s.n.* (MACB110661!). **Castilla y León:** Burgos, Sierra de San Millán, 17 September 1975, *Fuentes s.n.* (MACB5994!); León, Hayedo de Busmayor, 19 June 2019, *R. Vázquez s.n.* (MA939449!); León, Pinar de Lillo, 20 June 2019, *R. Vázquez s.n.* (MA939450!); Salamanca, entre San Miguel de Valero y San Esteban de la Sierra, 15 May 2016, *J.M. Gabriel y Galán & M. Puelles s.n.* (P00932168!). **Euskadi:** Álava, no date, *no collector s.n.* (MA226678!). **Madrid:** Rascafría, trail near Pradillo dam, 24 February 2019, *S. Molino et al. s.n.* (MA939451!). **Navarra:** Belagua, towards Lapatia pass, 26 August 2019, *J.M. Gabriel y Galán & M. Puelles s.n.* (MA939452!). **UNITED KINGDOM. Scotland:** Loch Katrine, 26 June 1901, *E.T. Harper & S.A. Harper s.n.* (C0379962F!).

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