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Subspecies of *Hypolepis rugosula* (Dennstaedtiaceae; Pteridophyta) around the world: morphological and biogeographic perspectives

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ABSTRACT

The "*Hypolepis rugosula* complex" has been the subject of great debate among pteridologists: some have considered *H. rugosula* a single subcosmopolitan (or circum-Antarctic) species, whereas others have considered it a species--complex, encompassing several species. In the 1920s and 1930s, four geographically distinct varieties of *H. rugosula* were recognized. In this work, we present a new taxonomy (with new combinations and statuses, as well as typification and full synonymy), together with complete distribution data for the species, with an infraspecific classification based on morphological and biogeographic perspectives. *Hypolepis rugosula* occurs in southern temperate regions and high-elevation tropical regions of the Americas, Africa (including Madagascar), Oceania and the Philippines, as well as in some isolated oceanic volcanic islands (*e.g.*, Saint Helena and Tristan da Cunha). Here, 15 geographically distinct subspecies are recognized. All subspecies are geographically segregated from each other, except in New Zealand, where two occur sympatrically—possibly due to two different arrival and colonization times. Four patterns of "indument" (referring to catenate and glandular hairs collectively) are distinguished. Different lineages are successful in their respective habitats; we observed two lineages with different ploidy levels (tetraploid and octoploid). Although long-distance dispersal is the best explanation for the extant distribution of *H. rugosula*; we do not exclude vicariance as a possible explanation for their occurrence on the land masses that were once united as Gondwana. Therefore, we are assuming that a fern species could remain unchanged for more than 70 Myr, and we are adopting the refugia theory, albeit with a different focus.

Key words: Cold refugia, *Phegopteris rugosula*, *Polypodium rugosulum*, taxonomic revision, widely distributed ferns

Introduction

Hypolepis rugosula (Labill.) J. Sm. was originally described as *Polypodium rugosulum* by Labillardière (1806), based on a plant collected in van Diemen's Land (now Tasmania) during the *Voyage* à la Recherche de la La Pérouse (La Pérouse's Research Expedition), made between 1791 and 1793 (Labillardière 1800, 1802, 1806; Stafleu & Cowan 1979; Brownsey & Chinnock 1984, 1987; Schwartsburd & Prado 2011).

Kaulfuss (1824) attributed the concept of cosmopolitanism (or at least circum-Antarctic distribution) to this species, also identifying plants from Chile as *Polypodium rugosulum* Labill. He was then seconded by Hooker & Arnott (1841), Gay (1853), and Brackenridge (1854). Brackenridge (1854: 18) also stated, ". . . we had some doubts at first, as to the identity of our New Zealand plant with the one from Chili [sic]; but a careful comparison has convinced us that they are one and the same species . . ." This concept was subsequently complemented by other authors, who gradually increased the knowledge of the range of *Polypodium rugosulum* (= *Hypolepis rugosula*): Moore (1857) included several names under the synonymy of *Pol. rugosulum*; Hooker (1862) considered it subcosmopolitan, recording it from Tasmania, Australia, New Zealand, Norfolk Island, India, Java, China, Ceylon, Chile, Ecuador, Peru and the Juan Fernandez Islands, as well as from the islands of Norfolk, Santa Helena, Tristan da Cunha, Bourbon (Réunion) and Fernando Po (Bioko); Mettenius (1858; 1865—as *Phegopteris rugosula* (Labill.) Fée) also recorded it from *Ostindien* ("East Indies"—i.e., Southeast Asia); Cordemoy (1891) recorded it for Réunion Island; Dobbie & Crookes (1951) recorded and described it in detail from New Zealand, as well as from South Africa and Japan; Brade (1956—then as *Hypolepis rugosula*) recorded it from the highlands of southeastern Brazil; Tardieu-Blot (1958—as *H. villoso-viscida* (Thouars) Tardieu) recorded it from the highlands of Belgian Congo; and Tryon & Tryon (1982—again as *H. rugosula*) recorded it from "the Americas". Consequently, the name *H. rugosula* has been adopted by others (Cronk 1989; Agnew & Agnew

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1994; Velayos *et al.* 2008; Schwartsburd 2010). Expressing a different point of view, other authors have considered *P. rugosulum* a species-complex. Such authors have considered *P. rugosulum sensu stricto* restricted to Australia and Tasmania and have named/described several other similar species from elsewhere: Petit-Thouars (1808; 1811) and Carmichael (1818) for Tristan da Cunha; Roxburgh (1816) for Saint Helena (although also recording *P. rugosulum* there); Kunze (1837; 1848; 1850) for Saint Helena, the Philippines, and Australia; Fée (1852; 1854-1857) for Saint Helena and Chile; Jenman (1881; 1892) for Jamaica; Philippi (1881) for Chile (although also recording *P. rugosula* there); Colenso (1883 [1884]) for New Zealand; Hicken (1906) for Argentina; Underwood & Maxon (1930) for Jamaica; Reimers (1934) for Madagascar and western Africa; Copeland (1942) for New Guinea; Wakefield (1955; 1956), Rawlings (1974), Brownsey & Chinnock (1984; 1987), and Brownsey *et al.* (1985) for Australia and New Zealand; Brownsey (1987) for southeastern Asia; Proctor (1985) for Jamaica; Meurk *et al.* (1994) for Campbell Island; Moran (1995) for Costa Rica; Verdcourt (2000) for the highlands of tropical east Africa; Roux (2001; 2009) for South Africa and Madagascar; Mickel & Smith (2004) for Mexico; Autrey *et al.* (2008) for the Mascareignes Islands; and Ponce *et al.* (2008) for Argentina and Chile. However, except for Brownsey & Chinnock (1984; 1987), few authors have drawn comparisons between the specimens studied and *P. rugosulum sensu stricto.* A third point of view, even "lumpier" than the first, is that of Hooker & Baker (1868), Bentham & Mueller (1878), Hillebrand (1888), Diels (1902? [not explicit]), Christensen (1906), van Alderwerelt van Rosenburgh (1908), Domin (1915), Cheeseman (1925), and Clifton (1997—with uncertainties), who have included *Polypodium rugosulum* under *P. punctatum* Thunb. (= *Hypolepis punctata* (Thunb.) Mett.; type from Japan), as a synonym, variety, or subspecies, considering it to be even more widely distributed.

The balanced concept was reached by Christensen and Skottsberg (Christensen 1920, 1931 [1932], 1932, 1934, 1937, 1940; Skottsberg 1920-1956, 1935; Christensen & Skottsberg 1920) who considered *Hypolepis rugosula* a circum-Antarctic species, recognizing four geographically distinct varieties: *H. rugosula* "var. *typica*" C. Chr., for Australia; *H. rugosula* var. *poeppigii* (Kunze) C. Chr., for Chile (including the Juan Fernandez Islands); *H. rugosula* var. *villoso-viscida* (Thouars) C. Chr., for Tristan da Cunha; and *H. rugosula* var. *africana* C. Chr., for Madagascar. Christensen & Skottsberg's balanced concept was then adopted by others, such as Alston (1959), Pizarro (1959), Schelpe (1970), Kornaīs (1979), Groves (1981), and Pichi-Sermolli (1983). Schwartsburd & Prado (2011) and Schwartsburd (2012a; 2012b) recently adopted Christensen & Skottsberg's concept. However, rather than using the varietal rank, those authors employed the subspecific rank, given that, at the macro level, the populations are virtually segregated and isolated from each other. They named *Hypolepis rugosula* subsp. *pradoana* Schwartsb. for the highlands of southern/southeastern Brazil; *H. rugosula* subsp. *poeppigiana* (Mett.) Schwartsb. & J. Prado *ined.* for Argentina and Chile (including the Juan Fernandez Islands); *H. rugosula* subsp. *africana* (C. Chr.) Schwartsb. & J. Prado for Madagascar and Réunion Island; *H. rugosula* subsp. *pichi-sermolliana* Schwartsb. & J. Prado for the highlands of central Africa and Bioko; and *H. rugosula* subsp. *rugosula* for Australia and Tasmania.

The present paper is a continuation of the abovementioned studies, treating nearly all populations of *Hypolepis rugosula* recognized to date, on the basis of the morphological and biogeographic data. We will show that *H. rugosula* is far more widely distributed than previously thought by Christensen (1920; 1932; 1937) and Christensen & Skottsberg (1920), although not exactly as interpreted by others, such as Hooker (1862).

Material and methods

We analyzed 515 sheets of *Hypolepis rugosula*, obtained from the following herbaria: the Berlin-Dahlem Botanical Garden and Museum, in Berlin, Germany (code, B); the National Institute of Agricultural Technology, in Buenos Aires, Argentina (code, BAB); the University of Barcelona CeDoc Institute of Plant Biodiversity, in Barcelona, Spain (code, BCN); the National University of Comahue, in Río Negro, Argentina (code, BCRU); the Federal University of Minas Gerais, in Belo Horizonte, Brazil (code, BHCB); the Natural History Museum, in London, England (code, BM); the National Botanic Garden, in Meise, Belgium (code, BR); the National University of Córdoba, in Córdoba, Argentina (code, CORD); the Natural History Museum, in Florence, Italy (code, FI), including the Pichi-Sermolli collection (FI-PS) and the Webb collection (FI-W); the Conservatory and Botanical Garden of the City of Geneva, in Geneva, Switzerland (code, G); the Rio Grande do Sul State Zoological Botany Foundation, in Porto Alegre, Brazil (code, HAS); the Bradeanum Herbarium, in Rio de Janeiro, Brazil (code, HB); the Royal Botanic Gardens, in Surrey, England (code, K); the Federal University of Rio Grande do Sul, in Porto Alegre, Brazil (code, ICN); the Leiden National Herbarium of the Netherlands, in Leiden, Netherlands (code, L); the V. L. Komarov Botanical Institute, in Saint Petersburg, Russia (code, LE); Saint Petersburg University, in Saint Petersburg, Russia (code, LECB); Museo de La Plata, in Buenos Aires, Argentina (code, LP); the Municipal Botanical Museum, in Curitiba, Brazil (code, MBM); the University of Oxford, in Oxford, England (code, OXF); the National Museum, in Prague, Czech Republic (code, PR); Charles University, in Prague, Czech Republic (code, PRC); the Rio de Janeiro Botanical Garden, in Rio de Janeiro, Brazil (code, RB); the National Museum of Natural History, in Santiago, Chile (code, SGO); the Botanical Museum, in Buenos Aires, Argentina

(code, SI); the Botanical Institute of São Paulo, in São Paulo, Brazil (code, SP); the University of São Paulo Herbarium of Phanerogamae, in São Paulo, Brazil (code, SPF); the Utrecht National Herbarium of the Netherlands, (now) in Leiden, Netherlands (code, U); the Federal University of Paraná, in Curitiba, Brazil (code, UPCB); Uppsala University, in Uppsala, Sweden (code, UPS); the Federal University of Viçosa, in Viçosa, Brazil (code, VIC); the Natural History Museum, in Vienna, Austria (code, W); and the Museum of New Zealand Te Papa Tongarewa, in Wellington, New Zealand (code, WELT). Living specimens of *H. rugosula* subsp. *pradoana* were studied in nature, at four different locations in Brazil. The complete list of the material examined appears in Appendix 1. The isolated populations are defined here as subspecies. Below each subspecies listed in the main text, only representative specimens are cited. Drawings were made (Fig. 1). The map shown in Fig. 2 was constructed with Diva-Gis, version 7.5 (http://www.diva-gis.org/download), the coordinates having been estimated with Google Earth (http://www.google.com/earth/download/ge/agree.html).

Results

In analyzing specimens of *Hypolepis rugosula* from nearly everywhere it occurs, we observed the following:

- *Hypolepis rugosula* is a subcosmopolitan species, with isolated populations throughout the southern temperate regions and tropical regions (at the upper elevations), as well as on isolated oceanic volcanic islands.
- *Hypolepis rugosula* is a unique species characterized by a combination of morphological characters (some almost exclusive) that distinguish it from all other species in the world.
- The subspecies are best defined geographically, and none present any striking exclusive morphological character.
- There are four well-defined patterns of "indument" (referring to catenate and glandular hairscollectively), which can be noted as tendencies ascribed to the subspecies.
- Some morphological characters are linked to local ecological factors and can vary within each subspecies, especially the frond size; the composition and thickness of the lamina; and the indument (thus the divisions among the four indument patterns are sometimes blurred).
- There are at least two successful lineages of *Hypolepis rugosula*: one tetraploid and one octoploid. The ploidy level seems unrelated to the indument pattern.
- Long-distance dispersal is the most likely explanation for the extant distribution of *Hypolepis rugosula* around the world, especially on the volcanic islands. However, we do not exclude the possibility of vicariance among the land masses that were once united as Gondwana.

Discussion

Morphology

Characters used in the delineation of the taxa

Morphology was the main basis of the species concept, from macroscopic features (*e.g.*, size of the frond, color of the axis, laminar architecture) to anatomical features (*e.g.*, stele and vascular bundles), microscopic features (*e.g.*, development of the pseudoindusia) and the indument pattern as the finest feature (especially, the types of hair, their sizes, in which lamina region they are present, *etc.*) This species concept is almost in total accordance with the actual state of art (*e.g.*, Bronwsey & Chinnock 1984; 1987; Brownsey 1987; Moran 1995; Mickel & Smith 2004; Schwartsburd 2012b; Schwartsburd & Prado unpublished data).

The sensitive difference of the present paper in relation to those cited above (and others) is that it accepts a morphological plasticity within *Hypolepis rugosula*—not only among the subspecies but especially within each subspecies. Although the indument is a reliable taxonomic character for most *Hypolepis* species, it must be carefully analyzed in *H. rugosula*. Individuals of *H. rugosula* typically bear both catenate-acicular and catenate-glandular hairs. However, the density of those hairs, as well as their number and position in the laminar regions, and even the co-occurrence of the two types of hair, are sometimes linked to local ecological factors.

Hypolepis rugosula is easily recognized by the color of the main axes (petioles, rachises, and pinna-rachises), which are burgundy (see Schwartsburd 2012b: Fig. 3D). This is almost an exclusive character, shared only with *H. distans* Hook. (a quite unique species); in all other species, the color is brown, ranging from straw-colored to dark brown (in a few species, they are purple, although only at the base of the petioles). Another feature that is probably exclusive is the vascular bundle of the petioles, which is proximally pi-shaped, and distally split into two S-shaped bundles. The other species present mostly omega-shaped vascular bundles proximally, distally splitting into many bundles (details in Schwartsburd 2012a; Schwartsburd & Prado unpublished data). In addition to these two features, the combination of the following characters serves to distinguish *H. rugosula* from all other species in the world: fronds small to medium in size—(15.0-)60.0-140.0 × (4.0-)20.0-50.0(-60.0) cm, main axes rugose and inermous, proximal pinnae equilateral and distant from the next pair , sori submarginal, pseudoindusia absent (the lamina margins occasionally revolute, protecting the sori, but never differentiated into hyaline flaps), and indument typically composed of catenate-acicular and catenate-glandular hairs (plus some brown hairs similar to those of the rhizome present throughout the main axes)—Fig. 1, A-R; see also Schwartsburd (2012b: Fig. 2).

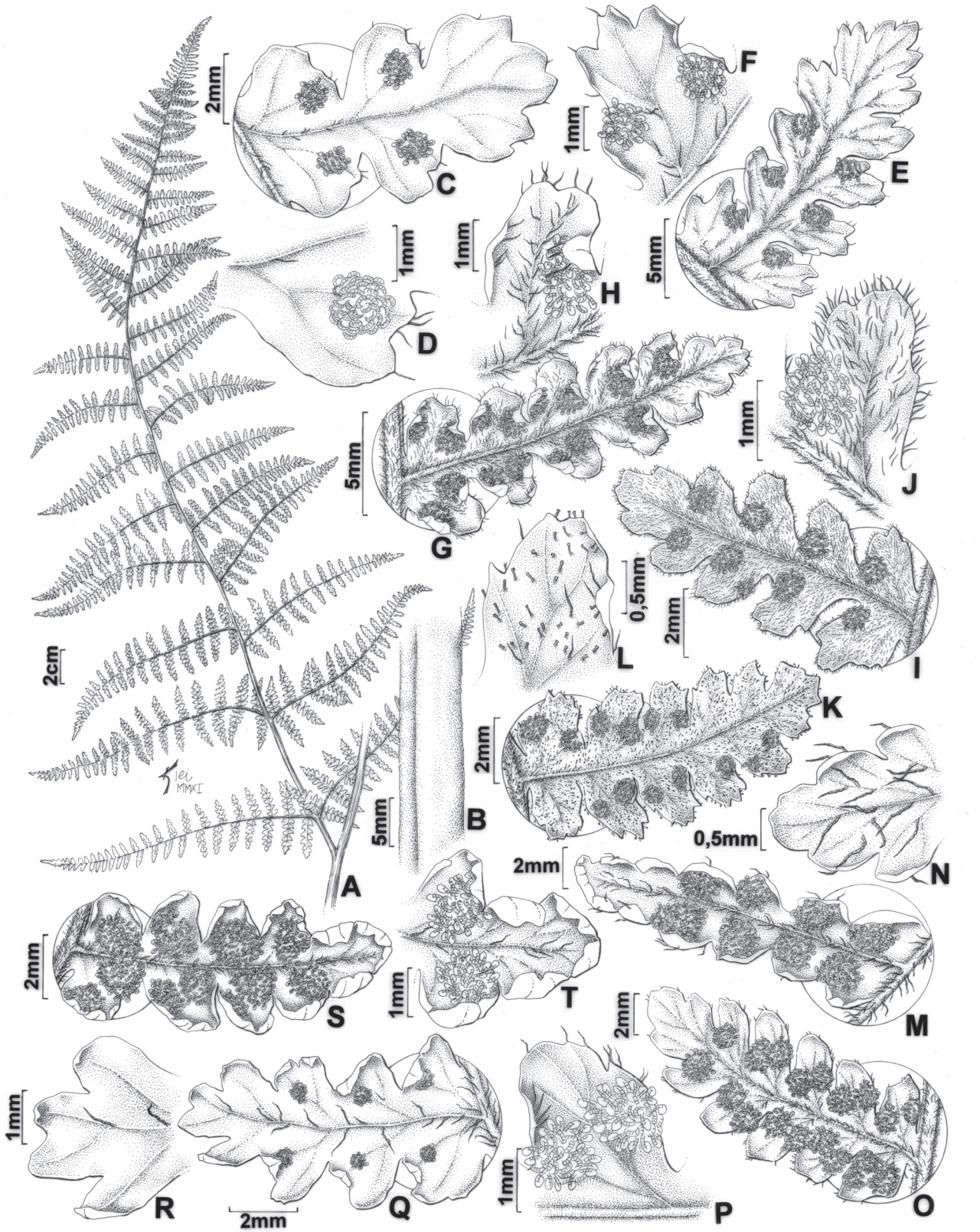

Figure 1. Some subspecies of *Hypolepis rugosula* (Labill.) J. Sm.: **A, B**—subsp. *poeppigiana* (Mett.) Schwartsb. & J. Prado (*Sota 2764*); **C, D**—subsp. *pradoana* Schwartsb. (*Brade 15540*); **E, F**—subsp. *poeppigiana* (Mett.) Schwartsb. & J. Prado (*Diem 702*); **G, H**—subsp. *poeppigiana* (Mett.) Schwartsb. & J. Prado (*Parra 106*); **I, J**—subsp. *rufobarbata* (Colenso) Schwartsb. (*Knight s.n.* [RB 215825 b]); **K, L**—subsp. *lactea* (Brownsey & Chinnock) Schwartsb. (*Knight s.n.* [RB 215825 a]); **M, N**—subsp. *rudis* (Kunze) Schwartsb. (*Cuming 140*); **O, P**—subsp. *rugosula* (*Burbidge 7423*); **Q, R**—subsp. *africana* (C. Chr.) Schwartsb. & J. Prado (*de MontBizon s.n.* [RB, ex Fée]); **S, T**—subsp. *viscida* (Roxb.) Schwartsb. & J. Prado (*Cuming 433*).

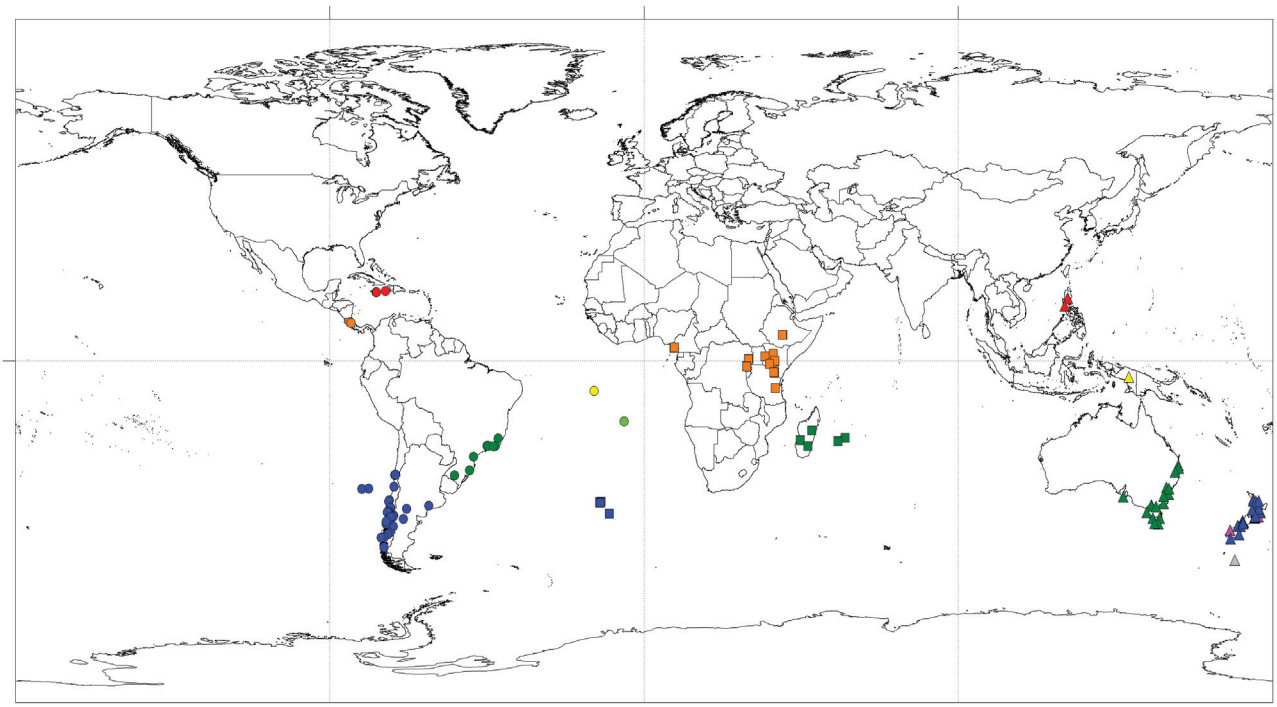

Figure 2. World map showing the distribution of the subspecies of *Hypolepis rugosula* (Labill.) J. Sm.: **red circle**—subsp. *pulcherrima* (L.M. Underw. & Maxon) Schwartsb. & J. Prado; **orange circle**—subsp. *colorata* (H. Christ) Schwartsb. & J. Prado; **blue circle**—subsp. *poeppigiana* (Mett.) Schwartsb. & J. Prado; **green circle**—subsp. *pradoana* Schwartsb.; **yellow circle**—subsp. *brownseyana* Schwartsb. & J. Prado; **bright green circle**—subsp. *viscida* (Roxb.) Schwartsb. & J. Prado; **blue square**—subsp. *villoso-viscida* (Thouars) Schwartsb. & J. Prado; **orange square**—subsp. *pichi-sermolliana* Schwartsb. & J. Prado; **green square**—subsp. *africana* (C. Chr.) Schwartsb. & J. Prado; **red triangle**—subsp. *rudis* (Kunze) Schwartsb.; **yellow triangle**—subsp. *archboldii* (Copel.) Schwartsb.; **green triangle**—subsp. *rugosula*; **blue triangle**—subsp. *rufobarbata* (Colenso) Schwartsb.; **pink triangle**—subsp. *lactea* (Brownsey & Chinnock) Schwartsb.; **gray triangle**—subsp. *subantarctica* (Brownsey & Chinnock) Schwartsb (colors only in PDF version).

Morphological plasticity within an isolated population

Sizes and degree of lamina division. Possibly, the frond sizes and degree of lamina division are related to the length and width of the rhizomes, and thus to the age of the plants. For example, mature fertile fronds of *Hypolepis rugosula* subsp. *pradoana* can be found ranging from 15.0 cm long, with pinnate-pinnatisect laminae (*Labiak 4778* [UPCB]), up to 95.0 cm long, with bipinnate-bipinnatisect lamina (*Schwartsburd 2310* [VIC])—see also Schwartsburd (2012b: Fig. 2). Similar variation can be observed on plants from Tristan da Cunha, for example: fronds 25.0 cm long, with pinnate-pinnatisect lamina (*Rogers* [K-000369143]); and fronds up to 60.0 cm long, with pinnate-bipinnatisect lamina (*Mejland 1158* [K]).

Lamina width and indument. Specimens from caves, or rocky/sheltered sites usually have thinly membranous laminae, almost flaccid, sparsely pilose to glabrous or completely glabrous. This can be seen, for example, in Tristan da Cunha (*Rogers* [K-000369141]), southeastern Brazil (*Brade 15540* [RB]—Fig. 1, C and D) and the Juan Fernandez Islands (*Sparre s.n.* [K], *Meyer 9536* [K]). However, specimens from open sunny areas tend to present laminae that are thicker, subchartaceous and much more densely pilose—see also the discussion of Christensen & Skottsberg (1920).

Indument patterns

The four basic indument patterns are easily distinguished, although the divisions between them can be blurred in specimens from sheltered places, which tend to present glabrescent or glabrous laminae, or in juvenile fronds, which tend to be much hairier. Apart from those exceptions, the four indument patterns are constant for most specimens of each subspecies of *Hypolepis rugosula*:

Typical. In the typical pattern, the laminar tissue between the veins is abaxially glabrous or nearly glabrous; laminar margins with catenate-acicular and catenate-glandular hairs sparsely throughout (Schwartsburd 2012b: Fig. 2), or with only catenate-acicular hairs, especially notable near the soral region (Fig. 1, C-H, O and P). This type is found in most subspecies: *colorata*, *poeppigiana*, *pradoana*, *pulcherrima*, *rugosula* and *subantarctica*.

Lacteal. In the lacteal pattern, the laminar tissue between the veins, abaxially, has conspicuous short catenate-glandular hairs; laminar margins copiously furnished with only catenate-glandular hairs (Fig. 1K, L). This pattern is found only in the subspecies *lactea*.

Rufobarbata. In the rufobarbata pattern, the laminar tissue between the veins, abaxially, has conspicuous reddish catenate-acicular hairs; laminar margins copiously

furnished with reddish catenate-acicular hairs (Fig. 1, I and J). This pattern is found in the subspecies *archboldii*, *rufobarbata* and *villoso-viscida*.

Africana. In the africana pattern, the laminar tissue between the veins is abaxially glabrous; laminar margins glabrous (Fig. 1, M, N and Q-T). This pattern is found in the subspecies *africana*, *brownseyana*, *pichi-sermolliana*, *rudis* and *viscida*.

In the other lamina regions, the four indument patterns are similar: main axes with catenate-acicular and catenate-glandular hairs (Fig. 1, C-T; Schwartsburd 2012b: Fig. 2); laminar tissue between the veins adaxially mostly with catenate-acicular hairs and sparse catenate-glandular hairs (Schwartsburd 2012b: Fig. 2C).

Cytology and ploidy

For the genus *Hypolepis*, the monoploid chromosome number (*x*) and haploid chromosome number (*n*) are 52 and 104 (*2n* = 104 and 208), respectively, where the latter number is likely attributable to tetraploidy (Brownlie 1957; Manton & Vida 1968; Smith & Mickel 1977; Brownsey 1983). Brownsey (1983) further suggested that the basic number would be an extinct *x* = 26 from a hypothetical ancestor, based on other Dennstaedtiaceae genera, and the "abnormal" species *H. distans* (*n* = 28) and *H. nigrescens* Hook. (*n* = 29) would have arisen from alloploidy. Following this idea, the extant regular species would have arisen from tetraploidy (*4n* = 104) or octoploidy (*8n* = 208).

Regarding the *Hypolepis rugosula* complex, Brownsey & Chinnock (1984) counted *n* = 52 for two specimens from New Zealand, which present the rufobarbata indument pattern (*Brownsey NZ 1435* from North Island) and the typical indument pattern (*Brownsey s.n.* [WELT—P11518 A and B], from Campbell Island). Following Brownsey (1983, *x* = 26), those numbers would represent tetraploid lineages (*4n* = 104). Because the two specimens present two distinct indument patterns, it is reasonable to suggest that the ploidy level is unrelated to the indument pattern.

Other chromosome counts were made by Manton & Vida (1968), who presented the numbers *2n* = 208 for Tristan da Cunha specimens, and *n* = ≈100 for those from Gough Island. Such numbers would then represent octoploid lineages (*8n* = 208). The one specimen analyzed in the present study (*Manton 5/66*, *4/66* [BM]) presents the rufobarbata pattern of indument.

Although it is too early to draw definitive conclusions, there are apparently at least two successful lineages within the *Hypolepis rugosula* complex (one tetraploid and one octoploid), and the ploidy level is probably unrelated to the indument pattern.

Biogeographic hypotheses and the adoption of subspecific rank

As many authors have argued (Brownsey 2001; Parris 2001; Wolf *et al.* 2001; Moran 2008), the distribution of fern taxa can be inferred to have happened by vicariance, dispersal or a combination of the two. Dispersal is the more widely accepted explanation, because ferns famously disperse their microspores by wind. Long-distance dispersal is also well accepted by the scientific community, being a common explanation for the origins of island floras (Tryon 1970; Moran 2008). However, vicariance tends to be avoided as an explanation for phenomena such as the Gondwana relationships. That is primarily due to our limited knowledge of the relationship between extant and extinct genera; often, "dispersal obscures evidence of vicariance" (Wolf *et al.* 2001). Because vicariance is avoided for explaining the distribution of families and genera, it is almost completely rejected at the species level.

The Dennstaedtiaceae is an extant cosmopolitan family that is one of the oldest families of leptosporangiate ferns (Smith *et al.* 2008). The oldest known fossils are at least 75 Myr old (Serbert & Rothwel 2003), from Canada. Although little is known about the Gondwana fossils, the family appeared in New Zealand at least 30 Mya (Mildenhall 1980, cited in Brownsey 2001)—before Gondwana had fully separated. Among its eleven extant genera, seven are subcosmopolitan (or at least amphitropical or circum-Antarctic): *Blotiella* R.M. Tryon, *Dennstaedtia* Bernh., *Histiopteris* J. Agardh, *Hypolepis* Bernh., *Microlepia* C. Prel, *Paesia* A.St.-Hil., and *Pteridium* Gled. ex Scop. (Tryon & Tryon 1982; Kramer 1990; Parris 2001; Smith *et al.* 2008). Some of its species present similar distribution: *Histiopteris incisa* (Thunb.) J. Sm. and *Microlepia speluncae* (L.) T. Moore are circum-Antarctic reaching the tropics (Parris 2001); *Hypolepis rugosula* is subcosmopolitan (Fig. 2; present paper); and *Pteridium aquilinum* (L.) Kuhn is cosmopolitan (*sensu* Tryon 1941).

The genus *Pteridium* is thought to contain only one species (Tryon 1941); two/three species, as well as two hypothetical allotetraploid species (Der *et al.* 2009; Thomson 2012); or up to a dozen species (Mickel & Smith 2004). There are also many infraspecific classifications that, in the interest of brevity, will not be discussed here. Nevertheless, the genus *Pteridium* is cosmopolitan and widely distributed throughout its range, and its isolated populations (= morpho-taxa: species, subspecies, or varieties) are interconnected. Therefore, it is reasonable to assume that its current distribution occurred by vicariance (see extensive discussion in Wolf *et al.* 2001: 267).

What about *Microlepia strigosa*, *Histiopteris incisa* and *Hypolepis rugosula*? Although they do present current subcosmopolitan distributions, their populations are all isolated from each other (Fig. 2). In addition, they seem quite rare in nature (our personal observation throughout Brazil). Certainly, no one has ever seriously considered these distributions to be a result of Gondwana vicariance but rather of long-distance dispersal. Would one species remain unchanged for more than 70 Myr? Or, even if speciation has occurred, would the same "successful design" be

maintained unchanged for 70 Myr in "cryptic species"? And furthermore, could three species within the same family share a coincidental "cryptic pattern"? One way to support the vicariance hypothesis for these three species is to invoke and adapt the Haffer-Vanzolini theory of refugia (Haffer 1992). These three Dennstaedtiaceae species currently occur in relatively southern temperate regions, including tropical regions, although their distribution in the latter is mostly limited to the upper elevations—commonly at ≥ 1000 m in subtropical regions, and at ≥ 2000 m in tropical regions (Brade 1956; Mickel & Smith 2004; Schwartsburd & Prado 2011; Schwartsburd 2012b). This is a common biogeographic pattern in which there is a similarity between upper elevations and the upper latitudes. It was conceived by the earliest biogeographers, such as Tournefort and Linnaeus (Papavero *et al.* 2013: Chap. 6), who termed it "altitudinal climatic zonation". Therefore, even though these species inhabit tropical regions, their occurrence is limited to temperate conditions. With this in mind, we can speculate that these species were more widely distributed during times when the Earth was cooler (*e.g.*, the last ice age) and are now relicts, restricted to cold refugia, as a result of climatic vicariance. Obviously, to interpret the current distribution of these three species as resulting from long-distance dispersal still seems much more reasonable, especially because they occur sympatrically on isolated oceanic volcanic islands (*e.g.*, Tristan da Cunha, Gough and Saint Helena). Given that volcanic islands are "young", their colonization by these species almost certainly occurred through long-distance, the spores traveling thousands of kilometers across the oceans to germinate and establish new populations. These plants seem adapted to long-distance dispersal. How many times such dispersal could have occurred is a question that cannot yet be answered. Did it occur during isolated events, such as the passing of super-hurricanes or El Niño? Do the populations often disperse their spores across the oceans on air masses or via jet streams? It is still too early to draw any conclusions about the origins of their distribution, which could be attributable to a combination of vicariance and dispersal.

Our basic hypothesis is that vicariance, dispersal or both occurred a long time ago and (in the case of dispersal) only a few times, thus providing a sufficient amount of time for the isolated populations of *Hypolepis rugosula* to start the process of speciation but not enough time for them to actually differentiate into separate species (given that they are still so similar). With this hypothesis in mind, we have recognized the geographically isolated populations as subspecies of *H. rugosula*.

The New Zealand hypothesis

Apart from the local ecological plasticity of indument, most subspecies of *Hypolepis rugosula* are quite homogeneous. The only place where two distinct patterns of indument (rufobarbata and lacteal) can be found is in New Zealand (on the North and South Islands, respectively). For New Zealand, we are adopting a secondary hypothesis: *H. rugosula* arrived there at two different times (on the South Island and on the North Island) and then became two well-defined isolated populations (subspecies), having now encountered each other and bred, creating "hybrids" (Brownsey & Chinnock 1984).

Taxonomic treatment

Hypolepis rugosula (Labill.) J. Sm., Bot. Mag. 3rd ser., 2: 8. 1846, as "*rugulosa*". *Polypodium rugosulum* Labill., Nov. Holl. Pl. 2: 92, t. 241. 1806 [1807?]. *Phegopteris rugosula* (Labill.) Fée, Gen. Filic.: 243. 1852, as "*rugulosa*". *Polypodium punctatum* Thunb. var. *rugosulum* (Labill.) Hook. & Baker, Syn. Fil.: 312. 1867, as "*rugulosum*". *Dryopteris punctata* (Thunb.) C. Chr. subsp. *rugosula* (Labill.) C. Chr., Index Filic.: 287. 1905. *Phegopteris punctata* (Thunb.) Mett. var. *rugosula* (Labill.) Hillebr., Fl. Hawaiian Island (Hillebrand): 563. 1888, as "*rugulosa*". *Dryopteris punctata* (Thunb.) C. Chr. var. *rugosula* (Labill.) Domin, Biblioth. Bot. 85: 41.1913. *Hypolepis rugosula* (Labill.) J. Sm. var. *rugosula* C. Chr. & Skottsb. *in* Skottsb., Nat. Hist. Juan Fernandez (Botany): 32. 1920, as "var. *typica*". Lectotype (designated by Pichi-Sermolli 1983: 260, and by Schwartsburd & Prado 2011: 157): [Tasmania], Habitat in Capite Van-Diemen, [1791-1793], *Labillardière s.n.* (FI-W!-214897; isolectotypes: FI-W!-214898, FI-W!-214899, FI-W!-on 2 sheets [214903, 214904], FI-W!-216239, FI-W!-218473, G!-on 2 sheets [00048249, 00048250], G!-on 2 sheets [00048252, 00048253], G!-00048255, LE!-2 sheets; probable isolectotypes: B! [ex Herb. Mertens], G!-00048251, K!, L!- 908837-403, PRC!). **Fig. 1A-T.**

Plants terrestrial, humicolous or epipetric. Rhizomes solenostelic and siphonostelic, (1.2-) 2.0-4.0 mm diam., lanose, the hairs catenate-acicular, yellowish to reddish-brown, 1.0-3.0(-4.0) mm long, 15-30-celled. Fronds erect or arched, with continuous growth, (15.0-)60.0-140.0 cm long; petioles (6.0-)20.0-50.0 cm × (0.8-)1.5-4.0 mm, proximally with one pi-shaped stele, distally with two S-shaped steles, burgundy, inermous, rugose, abaxially and adaxially sparsely villous with three or four kinds of hairs, the first kind of hair catenate-acicular, hyaline with reddish cross-walls, 0.3-0.7 mm long, 5-10-celled, the second catenate-glandular, hyaline with reddish cross-walls, 0.3-0.7 mm long, 5-10-celled, the third similar to those from the rhizomes, sparse and caduceus, the fourth (only in the rufobarbata pattern) catenate-glandular, entirely yellowish-brown, 1.0-2.5 mm long, 10-20-celled, scattered; laminae lanceolate or ovate, proximally pinnate-pinnatisect with segments pinnatifid up to bipinnate-bipinnatisect with pinnatifid segments, medially less decompound, distally pinnatisect, (10.0) 40.0-95.0 × (4.0-)20.0-50.0(-60.0) cm, with the two basal pair of pinnae much more distant from each other than from those above; rachises straight, burgundy throughout, or proximally burgundy and straw-colored

above, inermous, rugose, the indument similar to the petioles but the hairs more numerous, especially on the adaxial groove; proximal pinnae (2.0-)12.0-30.0 × (1.5-)4.0-12.0 cm, equilateral; costae abaxially sparsely villous, adaxially copiously villous, the hairs similar to those on the petioles and rachises but the third (and fourth) kind(s) usually absent or very scattered; costules abaxially and adaxially with the first and second kinds of hairs, or rarely with only the first or the second kind, shorter, 0.2-0.5 mm long, 4- to 7-celled; veins with the indument similar to the costules; laminar tissue between the veins abaxially glabrous or nearly glabrous (typical and africana-types), with the first kind of hair (rufobarbata pattern), or with the second kind (lacteal pattern), adaxially with both the first and second kinds of hair, ca. 0.2-0.3 mm long, 3- or 4-celled; lamina margins glabrous, with the first or second kind of hair, occasionally with both, similar in size to those on the laminar tissue between the veins; sori submarginal, unprotected or slightly protected; pseudoindusia absent, the lamina margin sometimes slightly revolute, protecting the sori, but never differentiated into a hyaline flap.
Distribution and ecology: Subcosmopolitan. The populations are segregated from each other (Fig. 2): Tasmania and Australia; New Zealand; the highlands of New Guinea; Luzon (the Philippines); Santa Helena Island; Ascension Island; Madagascar, Réunion Island, and Mauritius; Bioko and the highlands of central Africa (the Democratic Republic of Congo, Ethiopia, Uganda, Kenya, Tanzania and Rwanda); the islands of Tristan da Cunha and Gough; central and southern Argentina and Chile (including the Juan Fernandez Islands); the highlands of southern and southeastern Brazil; the highlands of Costa Rica; and the highlands of Mexico, Jamaica and Hispaniola. At sea level and above in temperate regions; above ca. 1000 m in subtropical regions; and above ca. 2000 m in tropical regions, having been reported at 3450 m and 3560 m, respectively, in Uganda and New Guinea.

Enumeration of the subspecies

Table 1 summarizes the subspecies considered here, their respective distribution and the pattern of indument. We present the subspecies taxonomically, on the basis of our examination of the representative materials, and provide details of their distribution.

1. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***pulcherrima*** (L.M. Underw. & Maxon) Schwartsb. & J. Prado, ***stat. nov.*** for *Hypolepis pulcherrima* L.M. Underw. & Maxon *in* Maxon, Proc. Biol. Soc. Wash. 43: 84. 1930, based on the description of Jenman, Bull. Bot. Dept. Jamaica 36: 10. 1892, sub "*Hypolepis purdieana* Hook". Lectotype (re-designated here): **JAMAICA.** Blue Mt. Range, elev., 7000 ft, VII/1878, *Jenman 72* (K!).
Distribution and ecology: Mexico, elev., 2100-2900 m (cited in Mickel & Smith 2004, no material seen); Jamaica and Hispaniola (Haiti), elev., 1500-2500 m.
Indument pattern: Typical.
Representative specimens examined: **JAMAICA.** Blue Mountain Peak, elev., 6500 ft, X/1952, *Proctor 7222* (U); Parish of St. Thomas, 18°02'N; 76°36'W, elev., ca. 1680 m, VII/1991, *Bellingham 1536* (BM). **HISPANIOLA. Haiti:** Massif de la Rotte, elev., 2375 m, IX/1928, *Ekman*, *Pl. Ind. Occid. H 10636* (BM).

Underwood & Maxon (1930) described *Hypolepis pulcherrima* as a new taxon indicating the description provided by Jenman (1892) for "*Hypolepis purdieana* Hook."—valid published under the International Code of Botanical Nomenclature (ICBN) art. 32.5 (ICBN 2006). Later, Lellinger (1977: 716) chose as lectotype one material cited by Underwood & Maxon (1930): *Maxon 9912* (US-on 4 sheets [image!]). According to ICBN (2006: art. 9.17), Lellinger should have chosen an original material of Jenman, if in existence. Thus, we here redesignate the lectotype: *Jenman 72* (K!).

2. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***colorata*** (H. Christ) Schwartsb. & J. Prado, ***stat. nov.*** for *Hypolepis repens* (L.) C. Presl var. *colorata* H. Christ *in* Pittier, Prim. Fl. Costar. 3(1): 37. 1901. Lectotype (designated here): **COSTA RICA.** Forêts au dessus de l'Achiote, au volcan de Poás, elev., 2000[-2200] m, XI/1896, *Tonduz 10704* (BR!; isolectotypes: G!-2 sheets [ex Herb. Boissier], G! [ex Herb. Dellesert], LE! [ex Herb. Inst. Phys.-Geogr. C.R.], LE! [ex Herb. Pittier & Durand], LE! [ex Herb. Tonduz], P-*n.v.*).
Distribution and ecology: Costa Rica, elev., 2000-2500 m.
Indument pattern: Typical.
Specimens examined: **COSTA RICA.** Alto del Sacatal, elev., 2500 m, I/1897, *Pittier 10529* (BR!, P-2 sheets-*n.v.*—syntypes of *H. repens* var. *colorata*); Volcan Poas, elev., 2300 m, III/1896, *Smith 6861* (B, G, K).

3. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***poeppigiana*** (Mett.) Schwartsb. & J. Prado, ***stat. nov.*** for *Hypolepis poeppigiana* Mett. *in* Hohen., Fil. Lechler. 1: 18. 1856. Lectotype (designated here): **CHILE. [Los Ríos]:** prope coloniam Arique in prov. Valdivia, V/1851, *Lechler*, *Pl. Chil. 194* (B!-20 0074790; isolectotypes: B!-20 0074789, B!-20 0074791, FI!, FI-W!-214914, G!-on 2 sheets, GOET-*n.v.*, K!-000640324, K!-000640325, K!-000640326, L!, LE!-2 sheets, UPS!, W!). **Fig. 1, A, B and E-H.**
Hypolepis chilensis Fée, Ic. Sp. Nouv.: 76. 1857 [1858?], *nom. superfl.* Syntypes: **CHILE. [Valparaíso]:** Valparaiso, [1834 or 1835], *Gaudichaud s.n.* [*31*?] (BR!, FI-W!-214906, FI-W!-214910, FI-W!-216216, G!, RB!, W!; probable duplicate: FI-W!-214917). **CHILE.** San Juan Fernandez, s.d., *Gay* (P?-*n.v.*, PC?-*n.v.*). **CHILE. [Los Ríos]:** près de la colonie Arique, province de Valdivia, [V/1851], *Lechler* [*Pl. Chil. 194*] (B!-3 sheets [20 0074789, 20 0074790, 20 0074791], FI!, FI-W!-214914, G!-on 2 sheets, GOET-*n.v.*, K!-000640324, K!-000640325, K!-000640326, L!, LE!-2 sheets, UPS!, W!).
Phegopteris poeppigii (Kunze) Fée ex Gay var. *hirsuta* Phil.,

Table 1. The subspecies of *Hypolepis rugosula* (Labill.) J. Sm., their distribution, and their indument pattern.

	Subspecies	Distribution	Indument
1	*pulcherrima*	Mexico, Jamaica, and Hispaniola	Typical
2	*colorata*	Costa Rica	Typical
3	*poeppigiana*	Central/southern Argentina and Chile (including the Juan Fernandez Islands)	Typical
4	*pradoana*	Southern/southeastern Brazil	Typical
5	*villoso-viscida*	Tristan da Cunha and Gough Islands	Rufobarbata
6	*viscida*	Saint Helena Island	Africana
7	*brownseyana*	Ascension Island (Saint Helena)	Africana
8	*pichi-sermolliana*	Central Africa and Fernando Po Island (Bioko)	Africana
9	*africana*	Madagascar, Reunion Island, and Mauritius	Africana
10	*rudis*	Luzon (the Philippines)	Africana
11	*archboldii*	New Guinea	Rufobarbata
12	*rugosula*	Australia and Tasmania	Typical
13	*lactea*	New Zealand	Lacteal
14	*rufobarbata*	New Zealand	Rufobarbata
15	*subantarctica*	Auckland and Campbell Islands	Typical

Anales Univ. Chile: 583. 1873 [1872?]. Lectotype (designated here): **[CHILE].** Puerto Lagunas, I/1872, *Simpson s.n.* (SGO-000000467 [image!]).
Hypolepis hauman-merckii Hicken, Anal. Soc. Cient. Arg. 62: 212, t. *s.n.* 1906. Lectotype (designated here): **ARGENTINA. Prov. Buenos Aires:** Sierra de la Ventana, 25/XII/1905, *Hauman-Merck s.n.* (SI-000095 [image!]).
Distribution and ecology: Central/southern continental Argentina and Chile, including the Juan Fernandez Islands (Más a Tierra and Más Afuera), and Chiloé Islands; elev., sea level up to ca. 800 m.
Indument pattern: Typical.
Representative specimens examined: **ARGENTINA. Buenos Aires:** Celle du Tandil, s.d., *Hauman-Merck s.n.* (SI?-*n.v.*—syntype of *Hypolepis hauman-merckii*). **Neuquén:** Correntoso, I/1935, *Cabrera & Job 227* (LP). **[Rio Negro]:** Puerto Blest, XI/1997, *Puntieri 396* (BCRU). **CHILE. [Coquimbo]:** Bosque Fray Jorge, elev., 500 m, VII/1938, *Andreas 856* (L, U). **[Valparaíso]:** Valparaiso, s.d., *Anonymous*, *n. 562* (W). **[Bío-Bío]:** Concepción, s.d., *Philippi s.n.* (K). **[La Araucanía]:** Prov. Cautín, Telmuco, 38°43'S; 72°35'W, elev., 150 m, VII/1939, *Montero 3696* (G). **[Los Ríos]:** Prov. Valdivia, II/1935, *Hosseus 113* (CORD). **[Los Lagos]:** Prov. Palena, I/1986, *Pedersen 14329* (BR, MBM). **[Aisén Gen. Carlos Ibañez del Campo]:** Patagonia Occid., Golfo de Peñas, VI/1908, *Skottsberg 302* (UPS). **Magallanes:** Puerto Edén, VII/1970, *Parra 106* (INTA). **CHILE, JUAN FERNÁNDEZ. Más a Tierra:** Valle Colonial, XII/1916, *Skottsberg & Skottsberg 120* (K, UPS). **Más Afuera:** Quebrada del Mono, elev., 400 m, II/1917, *Skottsberg & Skottsberg 439* (UPS). **CHILE, CHILOÉ. Chiloé [Isla Grande de Chiloé]:** s.d., *Cap. King s.n.* (K); [Dalcahue], Piruquina, X/1931, *Junge 32* (PRC, SI).

4. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***pradoana*** Schwartsb., Kew Bull. 67(4): 818, figs. 2A-E, 3C-D. 2012. Type: **BRAZIL. Rio de Janeiro:** Teresópolis, Parque Nacional da Serra dos Órgãos, Matas Nebulares and Campos de Altitude, Pedra do Sino, near Abrigo Quatro, on the way to the water tank, 22°27'42"S; 43°01'50"W, elev., 2120 m, 07/I/2011, *Schwartsburd & Pereira 2310* (holotype: SP!-on 3 sheets; isotypes: B!, FI!, G!, K!-on 3 sheets, LP!, NY!-on 2 sheets, P!-on 2 sheets, PRC!, RB!-on 2 sheets, SI!, SP!, UC!, UPCB!, VIC!, WELT!). **Fig. 1, C and D.**
Distribution and ecology: Highlands of southern/southeastern Brazil; elev., 1200-1800 m (southern Brazil) and 2000-2600 m (southeastern Brazil).
Indument pattern: Typical.
Representative specimens examined: **BRAZIL. Minas Gerais:** Passa Quatro, Itaguaré, elev., 2000 m, V/1948, *Brade & Araújo 19100* (RB). **Rio de Janeiro:** Itatiaia, P.N. Itatiaia, 22°21'47"S; 44°43'39"W, elev., 2200 m, VII/2009, *Schwartsburd et al. 2197* (SP, VIC). **Paraná:** Campina Grande do Sul, P.E. Pico do Paraná, 25°15'S; 48°50'W, [elev., 1876 m], VII/2008, *Labiak et al. 4778* (UPCB). **Santa Catarina:** Timbé do Sul, Serra da Rocinha, [elev., 1200 m], XI/1991, *Bueno s.n.* (ICN-155000). **Rio Grande do Sul:** Santa Cruz, XI/1911, *Jürgens 352*, *Rosenst. Fil. Austrobras. Exsic. II 77* (B).

5. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***villoso-viscida*** (Thouars) Schwartsb. & J. Prado, ***comb. nov.*** *et* ***stat. nov.*** for *Polypodium villoso-viscidum* Thouars, Esquisse Fl. Tristan d'Acugna: 33. 1803[1808]. *Hypolepis rugosula* var. *villoso-viscida* (Thouars) C. Chr., Sci. Results Norweg. Antarct. Exped. 1927-1928, n. 16: 15. 1937. *Hypolepis villoso-viscida* (Thouars) Tardieu *in* Humbert, Fl. Madagasc. 5(Polypodiacées, Tome 1): 6, f. I.3-5. 1958. Holotype: **TRISTAN DA**

CUNHA. s.d., *Petit-Thouars s.n.* (P-00522442 [image!]).
Cheilanthes viscosa Carmich., Trans. Linn. Soc. London 12(2): 511. 1818 [1819], *nom. superfl.* (for including *Polypodium villoso-viscidum* Thouars in synonymy). Lectotype (designated by Groves 1981: 404): **ISLAND OF TRISTAN DA CUNHA.** In the Wood, s.d., *Carmichael s.n.* (K!-000369140; isolectotype: BM!).
Distribution and ecology: Tristan da Cunha island group: Tristan da Cunha, Inaccessible, Nightingale and Gough; elev., sea level up to 400 m.
Indument pattern: Rufobarbata.
Representative specimens examined: **TRISTAN DA CUNHA.** Above Sandy Point, elev., 200 m, I/1938, *Mejland 1158* (K, L); 1924, *Rogers s.n.* (K-000369143); [from Tristan da Cunha] cultivated at Kew Gardens, 1968, *Manton 5/66*, *4/66* (BM). **INACCESSIBLE ISLAND.** Central part of plateau, elev., 400 m, II/1938, *Christophersen 2498* (K). **NIGHTINGALE ISLAND.** Trail to lake region, elev., 100 m, II/1938, *Christophersen 2233* (K); In a cave, 1924, *Rogers s.n.* (K-000369141). **GOUGH ISLAND.** Slope above Glen Creek, elev., 40 ft, XII/1955, *Wace 30* (BM); Creek banks on southern aspect of Tafel Koppie, 40°S; 09°W, elev., 270 m, XI/1979, *Roux 745* (K).

6. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***viscida*** (Roxb.) Schwartsb. & J. Prado, ***comb. nov.*** *et* ***stat. nov***. for *Polypodium viscidum* Roxb. *in* Beats., Tracts St. Helena [Beatson]: 319. 1816. Lectotype (designated here): **SAINT HELENA.** Sandy Bay, around stone dikes, 1813-1814, *Roxburgh 191/1* (BM!). **Fig. 1, S and T.**
Cheilanthes remota Kunze, Analecta Pteridogr.: 36. 1837, *nom. superfl.* (for including *Polypodium viscidum* Roxb. in synonymy). Type: **SANTA HELENA.** s.d., *Petersen* (herb.?; possible type: BR! [*Anonymous*, ex Herb. Martii]).
Hypolepis helenensis Fée, Mém. Foug., 5. Gen. Fil.: 147. 1852. Lectotype (designated here): **[SAINT HELENA].** Habitat in Insulâ Sanctae Helenae, [1841], *Cuming 433* (RB!-215823; isolectotypes: B!-20 0075256, B!-20 0075263, B!-20 0075264, B!-20 0075265, B!-20 0075268-, BM!, G!-2 sheets [ex Herb. Barbey-Boissier], G! [ex Herb. de Candolle], G! [ex Herb. Delessert], G! [ex Herb. Moricand], K!-000214965, K!-on 2 sheets [000350990 and 000350991], L!-0051757, L!-0051758-, LE!-2 sheets [ex Herb. Fischer], LE! [ex Herb. Petropol.], OXF!, UPS!, W! [ex Herb. Palat. Vindob], W! [ex Herb. Presl]).
Distribution and ecology: Saint Helena Island (Saint Helena); elev., commonly 600-820 m.
Indument pattern: Africana.
Representative specimens examined: **SAINT HELENA.** Valley near Willow Point, XII/1809, *Burchell 191* (B, K); Diana's Peak, VII/1813, *Roxburgh 23* (BM!—syntype of *Polypodium viscidum*?).

7. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***brownseyana*** Schwartsb. & J. Prado, ***subsp. nov.*** Type: **[SAINT HELENA. Ascension Island:** 1891?, *Anonymous* [unreadable] *s.n.* (holotype: K!-000650391).
Differs from *Hypolepis rugosula* subsp. *rugosula* by the glabrous (vs. pilose) lamina margins.
Distribution and ecology: Ascension Island (Saint Helena), elevation unknown (probably 400-800 m). Known only from the type collection.
Indument pattern: Africana.
Etymology: The subspecific epithet honors Dr. Patrick J. Brownsey, of the Museum of New Zealand, Te Papa Tongarewa Herbarium (WELT), who has made great contributions to pteridology, especially regarding the ferns of New Zealand and the Pacific. Dr. Brownsey has also reviewed in detail the *Hypolepis* species from those areas, expanding the knowledge and improving the understanding of this under-studied genus. Although our perception of the *Hypolepis rugosula* complex is somehow different than his, the present study is largely based on his works.

8. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***pichi-sermolliana*** Schwartsb. & J. Prado, Webbia 66(2): 158, figs. 1, 2. 2011. Type: **DEMOCRATIC REPUBLIC OF CONGO.** Dorsale ad ovest Del Lago Kivu, Montagne di Shamulamba, crinale a sud del rifugio del Groupe de Montagne de Kivu, elev., ca. 2600 m, 23/X/1953, *Pichi-Sermolli 4441* (holotype: FI-PS!--on 2 sheets [19686]; isotypes: FI-PS!-19441, FI-PS!-19665).
Distribution and ecology: Bioko (Equatorial Guinea), elev., 600-2130 m; continental Central Africa (the Democratic Republic of Congo, Ethiopia, Uganda, Kenya, Tanzania and Rwanda), elev., ca. 1800-3450 m.
Indument pattern: Africana.
Representative specimens examined: **BIOKO (EQUATORIAL GUINEA).** Elev., 7000 ft, 1860, *Maun 381* (K). **DEMOCRATIC REPUBLIC OF CONGO.** Kivu Nord, elev., 2700 m, VIII/1954, *Stauffer 122* (K); Vissoke Volcano, elev., 10,500 ft, XII/1930, *Burtt 3017* (K). **ETHIOPIA.** Bale Mountains, elev., 3400 m, II/1990, *Miehe & Miehe 2011* (K); Bale Massif, elev., 3000 m, III/1958, *Eriksson F 87b* (FI-PS). **UGANDA.** Ruwenzori, Bujuku Valley, elev., 3450 m, IV/1948, *Hedberg 646* (K); Western Province, Kigezi District, elev., 3000 m, XI/1954, *Stauffer 783* (K). **KENYA.** Embu District, elev., 2350 m, XII/1972, *Gillett & Holttum 20098* (K); Mount Kenya, elev., 10,000 ft, XII/1957, *Verdcourt 2063* (K, W). **TANZANIA.** Tanganyika, Kilimanjaro, elev., 2900-2950 m, III/1934, *Schlieben 4897* (B); S-Uluguru Mts., 2250-2350 m, XI/1972, *Pócs & Kornaīs 6828/J* (FI-PS). **RWANDA.** Kareba, elev., 3050 m, X/1974, *Auquier 4509* (FI-PS).

9. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***africana*** (C. Chr.) Schwartsb. & J. Prado, Webbia 66(2): 161. 2011. *Hypolepis rugosula* var. *africana* C. Chr. ex C. Chr., Dansk Bot. Ark. 7 (Pteridoph. Madagascar): 121. Jun 1932. *Hypolepis rugosula* var. *africana* C. Chr. *in* H. Perrier, Cat. pl. Madag., Pterid.: 49. 1931 [Feb 1932], *nom. nud. Hypolepis goetzei*

Hieron. ex Reimers *in* J. Mildbraed, Notizbl. Bot. Gart. Berlin-Dahlem 112(12): 189. 1934 (as "*Goetzei*"), *nom. nov. et stat. nov* for *Hypolepis rugosula* var. *africana* C. Chr. ex C. Chr. Lectotype (designated by Schwartsburd & Prado 2011: 161): **MADAGASCAR.** Süd-Betsiléo, Wald von Ankafina, III/1881, *Hildebrandt 4139* (B!-20 0075279; isolectotypes: B!-20 0075278, B!-20 0075283, BM!, LE!-2 sheets, P-2 sheets, G! [ex Herb de Candolle], G!-on 2 sheets [ex Herb. Barbey-Boissier], W!). **Fig. 1, Q and R.**
? *Phegopteris boryana* Mett. *in* Ettingsh., Farnkr. Jetztwelt: 161, 162, t. 98, fig 2., t. 102, fig. 2, t. 103, fig. 4. 1865. Syntypes?: **MAURITIUS.** 1846-1848, *Boivin s.n.* (W!-133/78-29, W!-133/78-30); **RÉUNION.** s.d., *Bory de Saint-Vincent s.n.* (RB!-frag. [215817]).
Distribution and ecology: Madagascar, Réunion Island and Mauritius; elevation unknown.
Indument pattern: Africana.
Representative specimens examined: **MADAGASCAR.** Tanala, s.d., *Kitching s.n.* (K!—syntype of *Hypolepis rugosula* var. *africana*); Pic d'Ivohibe, s.d., *Humbert 3324* (BM!, C--*n.v.*, P-*n.v.*—syntypes of *H. rugosula* var. *africana*). **RÉUNION ISLAND [ÎLE BOURBON].** 1853, *Boivin B 813* (FI, G); s.d., *Cordemoy 41* (K).

10. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***rudis*** (Kunze) Schwartsb., ***comb. nov. et stat. nov.*** for *Cheilanthes rudis* Kunze, Bot. Zeit. 6(11): 213. 1848. *Hypolepis rudis* (Kunze) Mett. *in* Ettingsh., Farnkr. Jetztwelt: 160. 1865. Lectotype (designated here): **[PHILIPPINES]. [Luzon]:** in the Philippines, [Prov. Albay], [1841], *Cuming 140* (B!-20 0075269; isolectotypes: B! [ex Herb. Koenpreuss], FI-W!, G! [ex Herb. Moricand], K!-000492488, K!-000492495, LE! [ex Herb. Fischer], LE! [ex Herb. Petropol.], OXF!, RB!, W! [ex Herb. Mus. Wien], W! [ex Herb. Palat. Vindob]). **Fig. 1, M and N.**
Distribution and ecology: Luzon (the Philippines), elev., ca. 100 m.
Indument pattern: Africana.
Specimens examined: **PHILIPPINES. Central Luzon:** Prov. Bataam, Mt. Mariveles, 14°32'N; 120°29'E, elev., 350 ft, XII/1903, *Williams 294* (K).
The materials *Cuming 140* (G [ex Herb. Barbey-Boissier], G [ex Herb. Dellesert],) are taxonomically different from the other collections of *Cuming 140* (see above). Therefore, they are not considered here as isolectotypes. Such materials correspond to species allied to the *Hypolepis punctata* and *H. tenuifolia* (G. Forst.) Bernh. groups, respectively.

11. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***archboldii*** (Copel.) Schwartsb., ***stat. nov.*** for *Hypolepis archboldii* Copel., Univ. Calif. Publ. Bot. 18(10): 218. 1942. Type: **[NEW GUINEA].** [Dutch New Guinea, Mt. Wilhelmina, 7 km northeast of Wilhelmina-top, elev., 3560 m, subalpine forest, common in ground moss, IX/1938], *Brass & Meyer-Drees 9852* (holotype: MICH-*n.v.*; isotypes: BM-*n.v.*, FI-PS!, L!-0051755, UC [image!]).
Distribution and ecology: New Guinea, elev., ca. 3560 m.
Indument pattern: Rufobarbata.

12. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***rugosula***, **Fig. 1, O and P.**
Hypolepis rugosula (Labill.) J. Sm. var. *rugosula* C. Chr. & Skottsb. *in* Skottsb., Nat. Hist. Juan Fernandez (Botany): 32. 1920, as "var. *typica*".
Cheilanthes amaurorhachis Kunze, Linnaea 23: 242, 306. 1850. *Hypolepis amaurorhachis* (Kunze) Hook., Sp. Fil. 2: 62. 1852, as "*amaurorachis*". Lectotype (designated by Brownsey & Chinnock 1987: 9): **[TASMANIA].** Cultis Hortis Lipsiae ex Tasmania, s.d., *Anonymous s.n.* [*Kunze*?] (B!-20 0074521; possible isolectotypes: BR!, K! [ex Herb. Hooker], K! [ex Herb. Kew]).
Hypolepis australis N.A. Wakef., Vict. Naturalist 72: 95. 1955. Type: **AUSTRALIA. Eastern Victoria:** Arte River, 23 III/1941, *Wakefield 107* (holotype: MEL-*n.v.* [1512588]).
Distribution and ecology: Continental Australia (more common on the east coast, but also in the west), Kangaroo Island, King's Island and Tasmania, elev., 600-1500 m.
Indument pattern: Typical.
Representative specimens examined: **AUSTRALIA. Queensland:** Lamington N.P., elev., 1000 m, V/1977, *Parris & Croxal 6235* (K). **New South Wales:** Blackheath, 33°38'S; 150°19'E, elev., 660 m, III/1977, *Coveny & Roy 9190* (K, WELT). **Australian Capital Territory:** New Chum Road, Cotter Valley, III/1964, *Gray 7423* (MBM). **Victoria:** Peninsula Country Golf Club, near Franstone, 38°08'S; 145°11'E, X/1973, *Chinnock P781* (K). **AUSTRALIA, KANGAROO ISLAND.** ca. 4 km east of Cape Borda, XII/1957, *Schodde 528* (K). **TASMANIA, KING'S ISLAND.** 1802-1805, *Brown 16a* (K, LE). **TASMANIA [VAN DIEMEN'S LAND].** 1833, *Gunn s.n.* (BR, FI, LE); E of Wedge River, ca. 44 km W of Maydena, 42°43.3'S; 146°16.3'E, XII/2007, *Brownsey PJB-TAS 29* (WELT).

13. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***lactea*** (Bronswey & Chinnock) Schwartsb., ***stat. nov.*** for *Hypolepis lactea* Brownsey & Chinnock, New Zealand J. Bot. 22: 55, figs. 1B, 2A, 3D, 7B, 18B, 19B. 1984. Type: **NEW ZEALAND. Wellington:** Eastbourne, Butterfly Creek, around fallen log, disturbed ground on creek bank, in beech forest, [41°18'S; 174°54'E], 21/II/1979, *Brownsey NZ 1356* (holotype: WELT! [P11516a]; isotype: CHR-*n.v.*). **Fig. 1, K and L.**
Distribution and ecology: New Zealand: North, Middle, and South Islands; elev., 150-300 m.
Indument pattern: Lacteal.
Representative specimens examined: **NEW ZEALAND, NORTH ISLAND**. **South Auckland:** Kauaeranga Valley, elev., 500 ft, I/1971, *Croxall & Parris 1479* (K). **Rodney County:** Kaipara Hills, 36°25'S; 174°30'E, elev., 140 m, I/1987, *Young s.n.* (WELT [P 17888a-c]). **Wellington Prov.:** East of Masterton, Stronvar, 41°04'S; 175°56'E, elev., 300 m, III/2008, *Bronwsey s.n.* (WELT [P 022219]). **NEW ZEA-**

LAND, MIDDLE ISLAND. s.d., *Strange s.n.* (LE *p.p.*). **NEW ZEALAND, SOUTH ISLAND. Greymouth:** 1875-1885, *Helms*, *N.Z.E. 49 p.p.* (L-384114). **Fiordland:** Milford Sound, XII/1989, *Smith-Dodsworth s.n.* (WELT [P 18047a-b]).

14. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***rufobarbata*** (Colenso) Schwartsb., ***comb. nov.* et *stat. nov.*** for *Polypodium rufobarbatum* Colenso, Trans. & Proc. New Zealand Inst. 16: 347. 1884. *Hypolepis rufobarbata* (Colenso) N.A. Wakef., Vict. Naturalist 72: 159. 1956. Lectotype (designated by Brownsey & Chinnock 1984: 54): **NEW ZEALAND.** Waipawa County, between Norsewood and Danneverke, hills, skirts woods, 1882, *Colenso s.n.* (WELT! [P3346]; isolectotype: K!). **Fig. 1, I and J.**
Polypodium viscidum Colenso, Tasm. J. Nat. Sci. 2: 164. 1845 (*opus non vidi*; cited in Brownsey & Chinnock 1984) *nom. illeg.*, non Roxburgh (1816). Lectotype (designated by Brownsey & Chinnock 1984: 52): **NEW ZEALAND.** Open spots, mountains, near Waikare Lake, XII/1841, *Colenso s.n.* (WELT-*n.v.* [P3189]; probable isolectotype: K! ["*Colenso 269*"]).
Distribution and ecology: New Zealand: North, Middle, South, and Stewart Islands; elev., 400-2800 m.
Indument pattern: Rufobarbata.
Representative specimens examined: **NEW ZEALAND, NORTH ISLAND. Auckland:** 1859, *Hochstetter 36* (W). **South Auckland:** Mt. Pirongia, IV/1966, *Bedford s.n.*, *Ex Parris 514* (K). **Tongariro National Park:** Ohakune, X/1929, *Sledge 169* (K). **Taupo Co.:** 38°57'S; elev., 1180 ft, XII/1983, *Gardner 4009* (K). **Te Aroha:** Tawa-Rata forest, elev., 1600 ft, I/1966, *Parris 334* (K). **Kaukau:** Howraki Gulf, XII/1848, *Lyell s.n.* (K). **Taranaki:** Mt. Egmont N.P., elev., 2800 m, IV/1966, *Parris 475* (K). **Upper Hut:** Kaitoke Waterworks, II/1979, *Brownsey NZ 1359* (WELT); [from Murgaroa Swamp, Upper Hut], cultivated at Orari Gardens, XII/1979, *Brownsey NZ 1435* (WELT). **Wellington:** Akatarawa Saddle, elev., 1400 ft, X/1970, *Parris 954* (K). **Grey Co.:** North of Barrytown, 42°12'S, s.d., *Gardner 4492* (K). **NEW ZEALAND, MIDDLE ISLAND.** s.d., *Strange s.n.* (LE *p.p.*). **NEW ZEALAND, SOUTH ISLAND. Westland:** Valley of the Teremakau, 1889, *Cartwright s.n.* (OXF). **Canterbury:** Banks Peninsula, XII/1961, *Melville 5775* (K). **Greymouth:** 1875-1885, *Helms*, *N.Z.E. 49 p.p.* (L-384113, PRC). **NEW ZEALAND, STEWART ISLAND.** II/1910, *Leland et al. 317* (G, K).

15. *Hypolepis rugosula* (Labill.) J. Sm. subsp. ***subantarctica*** (Bronswey & Chinnock) Schwartsb., ***stat. nov.*** for *Hypolepis subantarctica* Brownsey & Chinnock, New Zealand J. Bot. 22: 57, figs. 4A, 10, 18C, 19D. 1984. Type: **[NEW ZEALAND, CAMPBELL ISLAND].** Cultivated at CHR (G 11407) from Campbell Island, *ex Given s.n.*, 26/III/1981, *Brownsey s.n.* (holotype: WELT!-on 2 sheets [P11518/A and P11518/B]; isotypes: AK-*n.v.*, CHR-*n.v.*).
Distribution and ecology: New Zealand: Campbell Island and Auckland Island (cited in Brownsey & Chinnock 1984, no material seen); elevation unknown.
Indument pattern: Typical.
Specimens examined: **NEW ZEALAND, CAMPBELL ISLAND.** Above Smoothwater Bay, III/1947, *Brockie s.n.* (WELT [P 7786]).

Final conclusions and future prospects

From the extant geographic distribution data, it is possible to comprehend how widely distributed *Hypolepis rugosula* is, as well as to speculate how it was distributed in ancient times. It is also possible to notice the high number of isolated populations around the world (= subspecies richness). There might also be more subspecies, the herbaria material for which was not accessible, especially throughout other oceanic islands and possibly in other places in the Philippines.

Based on the morphological and geographic data alone, the present paper is unique and important in that it aggregates all of the *Hypolepis rugosula* subspecies names (under the same species-complex) and provides a detailed account of the distribution. The taxonomy proposed here certainly is not final—it is actually the starting point for future works.

Given that we are entering into a collaboration with Drs. Patrick Brownsey and Leon Perrie from the Te Papa Museum of New Zealand, we strongly encourage future works involving molecular investigation and comparison of *Hypolepis rugosula* subspecies. Such studies should attempt to answer the following questions: Is there one center of origin of *H. rugosula*?; Which were (or are) the routes of migration?; Could the distribution in the Americas, Africa and Oceania be attributable to Gondwana vicariance?; Which matrix areas are involved in long-distance dispersal to oceanic islands, and how many such areas are there?; Do the various indument patterns constitute natural subgroups?; Is it possible to speculate on the age of the species and subspecies, and on why speciation is taking so long?; Does the taxonomy presented here best represent *H. rugosula*?; Are some of the subspecies better classified as species?; and Should varietal level also be incorporated as a third taxonomic level? Cytology will be also very useful to determine which subspecies are tetraploid and which are octoploid. Do they represent two or more consistent and distinct lineages—or are the two ploidies based on random individuals, not representing lineages? Can both occur together in the same isolated population? Are there ploidies other than tetraploid and octoploid?

Dubious names

Cystopteris elata Desv., Linnaea 6: 264. 1831.—Tardieu-Blot (1858) considered this to be a synonym of *Hypolepis villoso-viscida*. We have not analyzed the type of that name.
Cystopteris fragilis (L.) Bernh. var. *pubescens* Phil., Anales Univ. Chile 43: 582. 1873.—Rodríguez (1995) synonymized

this under *Hypolepis poeppigii* (Kunze) R.A. Rodr. Although we saw the image of the type at Herbarium SGO, we could not be certain of its identity.

Hypolepis juergensii Rosenst., *nom. nud.* We have not found this name in any publication; nor does any index list it as a 'name validly published'. One specimen assigned to this name was analyzed: **BRAZIL. Rio Grande do Sul:** Sta. Cruz, Linha Chaves, XI/1911, *Jürgens 352*, *Rosenst. Fil. Bras. Exsic. II 77* (B!, NY-*n.v.*). The specimen at Herbarium B represents *H. rugosula* subsp. *pradoana.*

Phegopteris punctata (Thunb.) Mett. var. *flaccida* Hillebr. *in* W.F. Hillebr., Fl. Hawaiian Islands (Hillebrand): 563. 1888. *Hypolepis flaccida* (Hillebr.) W.J. Rob., Bull. Torrey Bot. Club 39: 579. 1912. Lectotype (designated by Brownsey 1987: 271): **HAWAII.** s.d., *Baldwin s.n.* (B!-20 0074635).—Although this material certainly belongs to *H. rugosula* complex, there is serious doubt as to whether it is really from Hawaii (see Brownsey 1987). Another possibility is that *H. rugosula* could have arrived there but did not establish an effective population.

Polypodium tribrachiatum C. Presl—there is only one exsiccate with this name written by Presl: *Cuming 433* (W). This sheet is also an isolectotype of *Hypolepis helenensis* Fée. Presl's name is probably just a *herbarium name*; we could not find it validly published anywhere.

Dubious records

HAWAII—see above in Dubious names.

[SAMOA]. Chatam Island, s.d., *Travers s.n.* (K, W)—these materials resemble *Hypolepis rugosula*, showing a pattern of indument similar to the lacteal pattern, but are too poorly preserved to be accurately identified. Dobbie & Crookes (1951) also recorded *H. rugosula* from Chatam, but their concept does not totally agree with ours (they listed it also for Japan, for example). Further collections are needed in order to determine whether *H. rugosula* does actually occur in Chatam (possibly as an undescribed subspecies) or not.

SOUTH AFRICA—Roux (2001) recorded *Hypolepis villoso-viscida* from South Africa. Although we saw no material of *H. rugosula* from there, it is likely that it occurs there. Possibly, the best name to apply to this taxon is *H. rugosula* subsp. *africana.*

[VENEZUELA]. Caracas, s.d., *Bredemeyer s.n.* (B, W)—these materials clearly belong to the *Hypolepis rugosula* complex. In the materials at Herbarium W, the locality "Caracas" is overwritten with "St. Helena". According to Schwartsburd (2012a) and Schwartsburd & Prado (unpublished data), *H. rugosula* does not occur in Venezuela. This collection is most probably from Santa Helena, but since such mislabeling seems so strange, these materials are better left as dubious.

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APPENDIX 1 – Full examined material

Below is the totality of the specimens examined in this work. Coordinates inside square brackets were estimated.

1. *Hypolepis rugosula* subsp. ***pulcherrima*** (L.M. Underw. & Maxon) Schwartsb. & J. Prado. Lectotype: **JAMAICA.** Blue Mt. Range, [18.0392°; –76.5741°] elev., 7000 ft, VII/1878, *G.S. Jenman 72* (K!).

Specimens examined: **JAMAICA.** [18.0555°; –76,5812°], elev., 6000 ft, IX/1879, *G.S. Jenman "6"* (K); 1874-1879, *G.S. Jenman s.n.* (OXF [00072087]); Blue Mt. Peak, III/1885, *D. Morris 100* (BM); 17/VII/1897, *O. Hansen 28* (B); 1897, *O. Hansen s.n.* (BM); Sir John's Peak, [18.1230°; –76.6548°], 9/IV/1910, *M.D. Watt 6* (K, U); west slope of the Blue Mountain Peak, elev., 6500 ft, 08/X/1952, *G.R. Proctor 7222* (U); St. Andrew, south of the grand ridge of the Blue Mountains, small tributary headwaters of the Clyde River, 18°05'N; 76°39'W, elev., ca. 1580 m, 18/IV/1990, *P.J. Bellingham 1168* (BM-on 2 sheets); Parish of Portland, west of Sir John Peak on the grand ridge of the Blue Mountains, steep ridge hanks at headwaters of the Mabess River, 18°05'N; 76°38W, elev., ca. 1680 m, 10/VI/1990, *P.J. Bellingham 1262* (BM); Parish of Portland, northwest of Sir John Peak, headwaters catchment of the Mabess River, 18°05'N; 76°38W, elev., ca. 1740 m, 26/IV/1991, *P.J. Bellingham 1433* (BM); Parish of St. Thomas, north of the grand ridge of Blue Mountains, immediately northwest of Portland Gap, 18°02'N; 76°36'W, elev., ca. 1680 m, 03/VII/1991, *P.J. Bellingham 1536* (BM-on 2 sheets); Summit of the Blue Mountain Peak, elev., 2100-2200 m, 7-9/VII/1926, *W.R. Maxon 9912* (US-on 4 sheets [image!]—previous lectotype of *H. pulcherrima*). **HISPANIOLA. Haiti:** Massif de la Rotte, morne la Rotte, [18.3833°; –74.0253°], elev., ca. 2375 m, 13/IX/1928, *E.L. Ekman*, *Pl. Ind. Occid. H 10636* (BM).

2. *Hypolepis rugosula* subsp. ***colorata*** (H. Christ) Schwartsb. & J. Prado. Lectotype: **COSTA RICA.** Forêts au dessus de l'Achiote, au volcan de Poás, [10.2003°; –84.2000°], elev., 2000 [-2200] m, XI/1896, *A. Tonduz 10704* (BR!; isolectotypes: G!-2 sheets [ex Herb. Boissier], G! [ex Herb. Dellesert], LE! [ex Herb. Inst. Phys.-Geogr. C.R.], LE! [ex Herb. Pittier & Durand], LE! [ex Herb. Tonduz], P-*n.v.*).

Specimens examined: **COSTA RICA.** Alto del Sacatal, versant E du massif de Buena Vista, [10.1798°; –84.2362°], elev., 2500 m, I/1897, *Pittier 10529* (BR!, P-2 sheets-*n.v.*—syntypes of *H. repens* var. *colorata*); Forêts du Roble, massif du Volcan Irazu, [9.9938°; –83.8773°], elev., 2000 m, 10/VII/1891, *A. Tonduz 4173 bis* (BR); Volcan Poas, Prov. Alajuela, elev., 2300 m, III/1896, *J.D. Smith 6861* (B, G, K).

3. *Hypolepis rugosula* subsp. ***poeppigiana*** (Mett.) Schwartsb. & J. Prado. Lectotype: **CHILE. [Los Ríos]:** prope coloniam Arique in prov. Valdivia, [–39.8985°; –73.2394°], V/1851, *W. Lechler*, *Pl. Chil. 194* (B!-20 0074790 [ex Herb. Mettenius]; isolectotypes: B!-20 0074789 [ex Herb Mettenius], B!-20 0074791, FI!, FI-W!-214914, G!-on 2 sheets, GOET-*n.v.*, K!-000640324, K!-000640325, K!-000640326, L!, LE!, LE! [ex Herb. Petropol.], UPS!, W!).

Hypolepis chilensis Fée. Syntypes: **CHILE. [Valparaíso]:** Valparaiso, [1834 or 1835], *C. Gaudichaud s.n.* [*31*?] (BR!, FI-W!-214906, FI-W!-214910, FI-W!-216216, G!, RB!, W!; probable duplicate: FI-W!-214917). **CHILE. San Juan Fernandez:** *C. Gay* (P?-*n.v.*, PC?-*n.v.*). **CHILE. [Los Ríos]:** près de la colonie Arique, province de Valdivia, [V/1851],*W. Lechler* [*Pl. Chil. 194*] (B!-3 sheets [20 0074789, 20 0074790, 20 0074791], FI!, FI-W!-214914, G!-on 2 sheets, GOET-*n.v.*, K!-000640324, K!-000640325, K!-000640326, L!, LE!, LE! [ex Herb. Petropol.], UPS!, W!).

Phegopteris poeppigii var. *hirsuta* Phil. Lectotype: **[CHILE].** Puerto Lagunas, I/1872, *E. Simpson s.n.* (SGO-000000467 [image!]).

Hypolepis hauman-merckii Hicken. Lectotype: **ARGENTINA. Prov. Buenos Aires:** Sierra de la Ventana, [–38.1625°; –61.5912°], 25/XII/1905, *M. Hauman-Merck s.n.* (SI-000095 [image!]).

Specimens examined: **ARGENTINA. Buenos Aires:** Celle du Tandil, s.d., *M. Hauman-Merck* (SI?-*n.v.* - syntype of *Hypolepis hauman-merckii*). **Neuquén:** Correntoso, [–38.9872°; –68.0025°], 10/I/1935, *A.L. Cabrera & M.M. Job 227* (LP); Brazo Rincón, [–40.7352°; –71.7422°], XI/1985, *B. Polastry s.n.* (BCRU); [Villa la Angostura?], Quetrihué, [–40.7555°; –71.6434°], 06/VI/1943, *J. Diem 728* (SI). **Rio Negro:** Puerto Blest, picada a Pto. Cántaros, [–41.0289°; –71.8153°], 29/XI/1997, *J. Puntieri 396* (BCRU-on 2 sheets); Puerto Blest, picada a Pto. Cántaros, 29/XI/1997, *J. Chiapella & J. Puntieri s.n.* (BCRU). **CHILE. Coquimbo:** Bosque Fray Jorge, [–30.0312°; –71.3262°], elev., 500 m, 07/VII/1938, *C.H. Andreas 856* (L-on 2 sheets, U); Bosque de Talinay, [–30.0040°; –71.1607°], 08/II/1948, *C. Jiles 576* (SI). **Valparaíso:** Valparaiso, [–33.1538°; –71.5462°], s.d., *Anonymous* [unreadable, "*Bredger*"?] *562* (W). **Bío-Bío:** Prope Conception, [–36.9080°; –73.0088°], 1832, *H. Cuming 149* (BM); Concepción, Southern Chili [Chile], [–36.7792°; –72.9187°], s.d., *R.A. Philippi s.n.* (K); ad Portum Coronel, [–37.0198°; –73.0883°], 1866, *"Buehenau" s.n.*, *ex Herb. Martii* (BR-on 2 sheets). **La Araucanía:** Tolten forest, [–39.1714°;

–72.8980°], 10/I/1902, *H.J. Elwes s.n.* (K); Telmuco [Temuco?], Malquehue, [–38.8019°; –72.5104°], I/1905, *Anonymous [R.M. Middleton?] s.n.*, *ex Herb. Middleton* (G); Prov. Cautín, Telmuco, Cierro Ñielol, 38°43'S; 72°35'W, elev., 150 m, 15/VII/1939, *G. Montero 3696* (G-on 2 sheets). **Los Ríos:** Valdívia, [–39.8288°; –73.1161°], *Anonymous s.n.*, *ex Herb. Reed* (K); circa Valdivia, s.d., *Brudgel & Osorio 813* (FI-W); Valdivia, [–39.8961°; –73.0784°], s.d., *Krause s.n.*, *ex Herb. Fil. Christensen 2897* (BM); Valdivia, 24/VI/1898, *O. Buchtien s.n.* (G, L); Valdívia, 40°S [–40.0047°; –73.1234°], 01/II/1906, *O. Buchtien s.n.* (B ['084677']); near Arique, 7 leagues above Valdívia, *Anonymous 813* (K); Prov. Valdivia, "Pauquipulei", [–39.9440°; –73.5471°], elev., ca. 200 m, V/1926, *A. Hollermayer s.n.*, *Werdermann Pl. Chilensis n. 1880* (B-*n.v.*, U); Prov. Valdivia, "Pauquipulei", [–39.6617°; –73.3362°], elev., ca. 200 m, X/1928, *A. Hollermayer s.n.*, *Werdermann Pl. Chilensis n. 1940* (U); (as "X Región"), Prov. Valdivia, Camino de Corral a Amargos, 01/II/1935, *C.C. Hosseus 113* (CORD); Prov. Valdivia, Chaiguín, Corral, 39°57'S; 73°30'W, elev., 100 m, 19/XII/1953, [*B.*?] *Sparre &* [?] *Smith 280* (G); Valdivia, s.d., *Anonymous s.n.* (SI-22740). **Los Lagos:** Puerto Varas, [–41.3394°; –72.8580°], 26/I/1929, *C.M. Hicken 51* (SI); Puerto Montt, [–41.4721°; –72.7735°], s.d., [*R.A.* or *F.*?] *Philippi s.n.* (K); Puerto Montt, *Anonymous*, *ex Herb. Reed* (LE-on 2 sheets?); Prov. Llanquihue, Puerto Montt, Contao, Camino al Sur, [–41.3596°; –72.5720°], 12/I/1981, *G. Montero 12011* (G); Prov. Llanquihue, Dpto. Puerto Vargas, Volcán Osorno, 41°10'S; 72°30'W, elev., 500 m, 19/I/1971, *E. Weldt & R. Rodríguez 826/121* (G-on 2 sheets); as "Prov. Chiloé", Llanquihue, road from Hotel Ensenada to Cochamo and Laguna Patos, elev., 75 m, 21/III/1939, *J.L. Morrison 17569* (G, K); Santa Lucia, sur le Carretera "Austral", à 81 km de Chaiten, [–43.3409°; –72.3585°], elev., 200 m, 09/II/1985, *C. Evrard 10627* (BM-*n.v.*, BR, MO-*n.v.*); Prov. Palena, near Villa Sta. Lucía, [–43.6215°; –71.8160°], 29/I/1986, *T.M. Pedersen 14329* (BR, MBM). **Aysén del General Carlos Ibañez del Campo:** Aysén, [–45.2868°; –72.8575°], 11/II/1959, *Anonymous [Kunkel?] n. 2963* (G [as "f. *patagonica*"—type?]); Aysén, Pto. Aysén, 11/II/1959, *Anonymous* [*unreadable*] *n. 2692* (G-on 2 sheets); Prov. Aysén, Fjord Quitralco, 45°43'S; 73°25'W, 01/XII/1987, *K.H. Rechinger & W. Rechinger 63988* (W); Halbinsel Taitao, [Laguna San Rafael National Park], 46-47°S [–46.5008°; –74.4068°], II/1921, *M. Gusinde 460* (W); Patagonia Occid., Golfo de Peñas, Pto. Hale, [–46.5632°; –75.2995°], 09/VI/1908, *C. Skottsberg 302* (UPS). **Magallanes [or Natales?]:** Puerto Edén, [–49.1153°; –74.4315°], 23/VII/1970, *O. Parra 106* (INTA). **Department Unknown:** Locality unknown, *Philippi s.n.* (BM); Locality unknown, *Philippi "3"* (BM, G, K); Locality unknown, *H. Cuming s.n.* (OXF [as *"Cumming"*]); Locality unknown, 1833, *Anonymous* [*unreadable*] *s.n.* (K); Locality unknown, 1870, *Shazmann s.n.* (G); Locality unknown, *Anonymous s.n.* (W ['364981']); South Chile, VIII/1919(?), *Anonymous* [*unreadable*, "*Escherholz*"?] *s.n.* (LE, LECB); San Rafael, elev., 150 m, 16/II/1921, *F. Reichert s.n.* (SI-2 sheets [ex Herb. *Hicken 33* [as "16/III/1921"] *et 34*]); Melinka, elev., 20 m, 27/I/1938, *C.H. Andreas 473* (U).

CHILE, JUAN FERNÁNDEZ ISLANDS. Más a Tierra [Robinson Crusoe]: [–33.6565°; –78.7996°/–33.6298°; –78.8664°/–33.6515°; –78.8898°], Valle Colonial, 11/XII/1916, *C. Skottsberg & I. Skottsberg 120* (K, UPS); Kolonidalen, 03/IV/1917, *C. Skottsberg & I. Skottsberg 587* (UPS); Cumberland Bay, San Juan Bautista, in one of the Spanish Caves, at the Settlement, 13/XII/1965, *F.G. Meyer 9536* (K, LP, NA-*n.v.*); Grutas de los Patriotas, 10-25/II/1955, *B. Sparre 14* (K); San Juan Bautista, along road in Village, 33°37'S; 78°50'W, elev., 30 m, 11/I/ 1996, *U. Swenson 379* (UPS). **Más Afuera [Alejandro Selkirk]:** Quebrada del Mono, [–33.7612°; –80.7694°], elev., ca. 400 m, 12/II/1917, *C. Skottsberg & I. Skottsberg 439* (UPS). **Island Unknown:** "In sylvatica ad rivulorum marginae collinae", IV/1830 [or V/1830], *M. Bertero 1664* (G-2 sheets, K-3 sheets); *Anonymous [Bertero?] 1348* (K); *M. Bertero s.n.* (G-on sheets).

CHILE, CHILOÉ ISLANDS. Chiloé [Isla Grande de Chiloé]: [–42.9494°; –73.8340°], s.d., *Cap. King s.n.* (K-on 2 sheets); 1830, *R. Brown(?) s.n.* (BM); 08/IV/1868, *R.O. Cunningham 26* (K); "Yenam", 18/V/1868, *Anonymous* [probably *Cunningham*] *s.n.* (K [same sheet as *Cunningham 26*]); Castro [Dalcahue], Piruquina, [–42.3668°; –73.7887°], elev., 200 m, III/1924, *E. Werdermann*, *Pl. Chilensis n. 304* (G, SI, U); [Dalcahue], "Tiruquina" [Piruquina], [–42.3220°; –73.8470°], 04/X/1931, *C. Junge 32* (MO-*n.v.*, PRC, SI); [Dalcahue], Piruquina, 04/X/1931, *C. Junge 40* (L); 20/II/1971, *O. Zöllner 4779* (L).

ARGENTINA or CHILE. Department Unknown: Patagonia, ['–41.6050°; –68.8782°'], *F. Steindachner s.n.* (W ['9293']); Puerto Leopoldo, II/1921, *Hicken s.n.* (SI [ex Herb. Hicken 35]); Locality unknown, 22/I/1909, *P. "Nurett"*(?) *53* (SI).

4. ***Hypolepis rugosula*** subsp. ***pradoana*** Schwartsb. Type: **BRAZIL. Rio de Janeiro:** Teresópolis, Parque Nacional da Serra dos Órgãos, Matas Nebulares e Campos de Altitude, Pedra do Sino, próximo ao Abrigo Quatro, no caminho para a caixa d'água, 22°27'42"S; 43°01'50"W, elev., 2120 m, 07 Jan 2011, *P.B. Schwartsburd & J.B.S. Pereira 2310* (holotype: SP!-on 3 sheets; isotypes: B!, FI!, G!, K!-on 3 sheets, LP!, NY!-on 2 sheets, P!-on 2 sheets, PRC!, RB!-on 2 sheets, SI!, SP!, UC!, UPCB!, VIC!, WELT!).

Specimens examined: **BRAZIL. Minas Gerais:** Alto Caparaó, Parque Nacional do Caparaó, Pico da Bandeira, [20°26'S; 41°48'W], elev., 2600 m, 09/VII/2009, *P.B. Schwartsburd et al. 2000* (SP); Passa Quatro, Itaguaré, [22°25'S; 44°53'W], elev., 2000 m, 09/V/1948, *A.C. Brade & S. Araújo 19100* (RB); Locality unknown, *Anonymous [T. de Moura?] 59*, *ex Herb. Moura* (B). **Rio de Janeiro:** Itatiaia, Serra do Itatiaia, [22°23'S; 44°40'W], elev., 2000 m, VI/1913, *F. Tamandaré T. Jr. & A.C. Brade '839' vel '1837'* (RB); Itatiaia, Serra do Itatiaia, elev., 2000 m, 4-10/VI/1913, *F. Tamandaré T. Jr. & A.C. Brade 6501* (HB,

NY-*n.v.*, RB); Itatiaia, Pedra do Echo, [22°23'S; 44°40'W], elev., 2400 m, III/1937, *A.C. Brade 15540* (RB); Itatiaia, Estrada km 10, [22°21'47"S; 44°43'39"W], 21/XI/1948, *A.C. Brade 18882* (NY-*n.v.*, RB-*n.v.*, SP); Itatiaia, Estrada Nova km 11, [22°22'S; 44°42'W], elev., 2100 m, V/1950, *A.C. Brade 20288* (NY-*n.v.*, RB-*n.v.*, SP-on 2 sheets); Itatiaia, Planalto of Itátiaia, vicinity of Agulhas Negras, near Piedra Atar [Pedra do Altar], [22°22'29"S; 44°40'30"W], elev., 2300 m, 03/XI/1965, *R.M. Tryon & A.F. Tryon 6682* (GH-*n.v.* HB); Itatiaia, Planalto of Itátiaia, vicinity of Agulhas Negras, near Piedra Atar [Pedra do Altar], elev., 2300 m, 03/XI/1965, *R.M. Tryon & A.F. Tryon 6683* (GH-*n.v.*, HB); Itatiaia, Parque Nacional do Itatiaia, Pedra Assentada, [22°24'S; 44°40'W], elev., 2500 m, 07/VIII/2006, *J.P. Condack 513* (NY-*n.v.*, RB-*n.v.*, SP); Itatiaia, Parque Nacional do Itatiaia, Estrada para o Planalto entre os kms 9 e 10, 22°21'47"S; 44°43'39"W, elev., 2200 m, 18/VII/2009, *P.B. Schwartsburd et al. 2197* (SP); Nova Friburgo, Pico da Caledônea, 22°21'13"S; 42°35'13", elev., 2220 m, 15/VI/2004, *R.C. Forzza et al. 3412* (RB-*n.v.*, SP-2 sheets, SPF); Petrópolis, Parque Nacional da Serra dos Órgãos, Castelo do Açu, 22°29'08"S; 43°03'42"W, elev., 2100-2150 m, 10/I/2011, *P.B. Schwartsburd et al. 2323* (SP); Therezopolis [Teresópolis], 11/III/1938(?), *A.C. Brade s.n.*, *ex Herb. Mus. Nac. Rio Janeiro 21047* (BM-on 2 sheets, R-*n.v.*). **Paraná:** Campina Grande do Sul, Parque Estadual do Pico do Paraná, 25°15'S; 48°50'W, elev., 1500-1876 m, 09/VII/2008, *P.H. Labiak et al. 4778* (UPCB-on 2 sheets). **Santa Catarina:** Timbé do Sul, Serra da Rocinha, [28°48'S; 49°57'W], [elev., 1200 m], 04/XI/1991, *R.M. Bueno s.n.* (ICN-155000). **Rio Grande do Sul:** Santa Cruz, [−30.1847°; −54.2575°], XI/1911, *C. Jürgens 352*, *Rosenst. Fil. Austrobras. exsic. II 77* (B, NY-*n.v.*—type of *Hypolepis juergensii* Rosenst.?).

5. *Hypolepis rugosula* subsp. ***villoso-viscida*** (Thouars) Schwartsb. & J. Prado. Type: **TRISTAN DA CUNHA.** *A. du Petit-Thouars s.n.* (P-00522442 [image!]).
Cheilanthes viscosa Carmich. Syntypes: Island of Tristan da Cunha, in the Wood, *D. Carmichael s.n.* (BM!, K! [000369140]).

Specimens examined: **TRISTAN DA CUNHA.** Above Sandy Point, [−37.0897°; −12.3192°], elev., 200 m, 18/I/1938, *Y. Mejland 1158* (K, L); 1924, [−37.1065, −12.2309°], *H.M. Rogers s.n.* (K [000369143]).
INACCESSIBLE ISLAND. Central part of plateau, tree fern country, [−37.3017°; −12.6789°], elev., 400 m, 25/II/1938, *E. Christophersen 2498* (BM-*n.v.*, K, O-*n.v.*).
NIGHTINGALE ISLANDS. Trail to lake region, cliff in tussock grass, [−37.4220°; −12.4798°], elev., 100 m, 12/II/1938, *E. Christophersen 2233* (BM-*n.v.*, K, O-*n.v.*); west ridge to peak, moist cliff, [−37.4245°; −12.4828°], elev., 200 m, 10/II/1938, *E. Christophersen 2224* (K); in a cave, 1924, *H.M. Rogers s.n.* (K [000369141]).
GOUGH ISLAND. Slope above Glen Creek, 100 yds from Archway Rock, [−40.3595°; −9.9033°], elev., 40 ft, 05/XII/1955, *N.M. Wace 30* (BM); Slope above Lower Watersmeet, main Glen, 02/II/1956, *N.M. Wace 128* (BM); creek banks on southern aspect of Tafel Koppie, 40°S; 09°W, [−40.2919°; −9.9430°], elev., 270 m, 03/XI/1979, *J.P. Roux 745* (K).

6. *Hypolepis rugosula* subsp. ***viscida*** (Roxb.) Schwartsb. & J. Prado. Lectotype: **SAINT HELENA.** Sandy Bay, about stone dikes, 1813-1814, *J. Roxburgh 191/1* (BM!).
Cheilanthes remota Kunze. Type: **SANTA HELENA.** *C.W. Petersen* (herb.?; possible type: BR! [*Anonymous*, ex Herb. Martii]).
Hypolepis helenensis Fée. Lectotype: **[SAINT HELENA].** Habitat in Insulâ Sanctae Helenae, [1841], *H. Cuming 433* (RB! [215823]; isolectotypes: B! [20 0075256], B! [20 0075263], B! [20 0075264], B! [20 0075265], B! [20 0075268], BM!, G!-2 sheets [ex Herb. Barbey-Boissier], G! [ex Herb. de Candolle], G! (ex Herb. Delessert), G! [ex Herb. Moricand], K! [000214965], K!-on 2 sheets [000350990 and 000350991], L! [0051757], L! [0051758], LE!-2 sheets [ex Herb. Fischer], LE! [ex Herb. Petropol.], OXF!, UPS!, W! [ex Herb. Palat. Vindob], W! [ex Herb. Presl]).

Specimens examined: **SAINT HELENA.** Valley near the Willow Point, XII/1809, *Burchell 191* (B, K-2 sheets); Diana's Peak, [−15.9638°; −5.7116°], VII/1813, *J. Roxburgh 23* (BM—syntype of *Polypodium viscidum*?); 1832, *Lesson s.n.* (K [000214957]); 1860-1871, [−15.9282°; −5.6975°], elev., 2000 ft, *J.C. Mellifs s.n.* (B [20 0075274]); 1864, *"Maximovicz" s.n.* (LE); 1869, *M. Vieillard 142* (B-2 sheets); 1884, [−15.9815°; −5.7178°], *W. Ivest s.n.* (B); 29/VIII/1903, *Longwood s.n.* (B-3 sheets [20 0075329, 20 0075330, and 20 0075331]); 30/VIII/1903, *Longwood s.n.* (B [20 0075332]); common at ≥ 1800 ft, III/1956, *A.R. Ken 30* (K); Diana's Peak, s.d., *L. Dalhousie s.n.* (G-on 3 sheets); s.d. *I. Buchanan 146* (B); s.d., *Brehmer s.n.* (B-2 sheets); s.d., *Wellis s.n.* (B-2 sheets [20 0075266 and 20 0075270], OXF); s.d., *Perrotel s.n.* (W); s.d., *"Lefroy" s.n.* (K [000214956]); s.d., *Boos s.n.* (W); s.d., *Labscheid* s.n. (W); s.d., *Nuttal s.n.* (K [000214955]); s.d., *J.D. Hooker s.n.* (K [000214960]); s.d., *W. Robinson s.n.* (K [000214964]); s.d., *Anonymous*, *ex Herb. Forsyth.* (K [000214958]); s.d., *Anonymous* (B [20 0075260]); s.d., *Anonymous* (B! [20 0075271—type of *Ch. remota*?]); s.d., *Anonymous*, *ex Herb. Kew 883* (FI); s.d., *Anonymous* (K [000214961]); s.d., *Anonymous* (K [000214963]).

7. *Hypolepis rugosula* subsp. ***brownseyana*** Schwartsb. & J. Prado**.** Type: **[SAINT HELENA]. Ascension Island:** [−7.9517°; −14.3474°], 1891?, *Anonymous* [unreadable] *s.n.* (holotype: K!-000650391).

8. ***Hypolepis rugosula*** subsp. ***pichi-sermolliana*** Schwartsb. & J. Prado. Type: **DEMOCRATIC REPUBLIC OF THE CONGO:** Dorsale ad ovest Del Lago Kivu, Montagne di Shamulamba, crinale a sud del rifugio del Groupe de Montagne de Kivu, elev., ca. 2600 m, 23/X/1953, *R.E.G. Pichi-Sermolli 4441* (holotype: FI-PS!-on 2 sheets [19686]; isotypes: FI-PS! [19441], FI-PS! [19665]).

Specimens examined: **BIOKO (EQUATORIAL GUINEA).** s.d., [3.3432°; 8.6255°], *Maun s.n.* (K); s.d., *Maun s.n.* (W); elev., 7000 ft, [3.5747°; 8.7620°], 1860, *Maun 381* (K).
BELGIAN CONGO (DEMOCRATIC REPUBLIC OF THE CONGO). Kivu Nord, Virunga Westgruppe, [−1.4310°; 29.4643°], elev., ca. 2700 m, 21/VIII/1954, *H.U. Stauffer 122* (K); Vissoke Volcano, [−1.5243°; 29.4529°], elev., 10,500 ft, 15/XII/1930, *B.D. Burtt 3017* (K-on 2 sheets).
ETHIOPIA. Bale Mountains, above Rira, [6.7778°; 39.7540°], elev., 3400 m, 08/II/1990, *G. Miehe & S. Miehe 2011* (K-on 2 sheets); Bale Massif, [6.7785°; 39.7281°], elev., 3000 m, 22/III/1958, *J. Eriksson F 87b* (FI-PS); 59 km S of Goba along the road across the Sanetti Plateau to Dolo Mena, just below Rira, [6.8560°; 39.6464°], elev., 3250 m, 15/IX/2005, *I. Friis et al. 12074* (K-on 3 sheets).
UGANDA. Ruwenzori, [0.4120°; 30.0142°], elev., 9000 ft, 04/X/1905, '*Baeor*'(?) *569* (K); id., Bujuku Valley, near Bigo camp, [0.3658°; 29.9442°], elev., 3450 m, 02/IV/1948, *O. Hedberg 646* (K); Western Province, Kigezi District, Virunga Ostgruppe, [−1.4503°; 29.4218°], elev., ca. 3000 m, 14/XI/1954, *H.U. Stauffer 783* (K).
KENYA. Murang'a, Nyandarua Districts, Kimakia forest station, [−0.7453°; 36.7692°], elev., 2475 m, 13/VII/1969, *R.B. Faden & A. Evans 69/897* (K-on 2 sheets); Embu District, above Castle Forest Station, [−0.3021°; 37.4097°], elev., ca. 2350 m, 19/XII/1972, *J.B. Gillett & R.E. Holttum 20098* (K); id., Versante meridionale del Monte Kenya, [−0.0480°; 37.2864°], elev., 2700-3000 m, 13/XII/1966, *R.E.G. Pichi-Sermolli 6892* (FI-PS); id., Versante meridionale del Monte Kenya, elev., 1800 m, 12/XII/1966, *R.E.G. Pichi-Sermolli 6865* (FI-PS); Samburu District, Mt. Nyiru, [1.8230°; 37.0238°], elev., 7000 ft, 13/XII/1972, *J.B.C. Cameron 139* (K); Mount Kenia, elev., 10,000 ft, 13/XII/1957, *B. Verdcourt 2039* (K-on 2 sheets); id., 15/XII/1957, *B. Verdcourt 2063* (K-on 2 sheets, W); NE Elgon, [1.1881°; 34.6244°], elev., 9500 ft, IV/1959, *Tweedie 1810* (K-on 3 sheets); Mount Elgon, Kitale, 27/XII/1960-01/I/1961, *H. Löffler E-39* (W); id., 27/XII/1960-01/I/1961, *H. Löffler E-115* (W); North Nyeri District, Mt. Kenia, elev., 9500 ft, 06/IX/1963, *B. Verdcourt 3727* (K); Western slopes of Mount Kenia, elev., ca. 3000 m, 28/IX-07/X/1909, *E.A. Mearns 1698* (K); Nyeri District, Aberdare Mountains, Kiandongoro, [−0.5348°; 36.7074°], elev., 3020 m, 24/X/1971, *R.B. Faden & A.J. Faden 71/886* (FI-PS-on 2 sheets, K-on 2 sheets); Meru District, Volcanic cone Kirui, on the slopes of Ithanguni, [−0.0768°; 37.5316°] elev., ca. 2530 m, 28/II/1970, *R.B. Faden & A. Evans 70/116* (FI-PS, K-on 2 sheets); Narok District, Masailand, [−0.8807°; 36.0429°], elev., ca. 7100 ft, 11/VII/1961, *Glover et al. 2048* (FI-PS, K).
TANZANIA. Kilimanjaro, Umbwe route, [−2.9801°; 37.4241°] elev., 2800 m, 16/I/1997, *A. Hemp 1432* (K-on 2 sheets); id., above Nrwaa, [−3.2272°; 37.4385°], elev., 2300 m, 03/III/1997, *A. Hemp 1608* (K-on 2 sheets); Tanganjika, Kilimandscharo, [−2.9864°; 37.1899°], elev., 2900 and 2950 m, 07/III/1934, *H.J. Schlieben 4897* (B-5 sheets); S-Uluguru Mts., E slope of Lunkwangule plateau, [−7.1827°; 37.6634°], elev., 2250-2350 m, 13/XI/1972, *A.T. Pócs & J. Kornaīs 6828/J* (FI-PS).
RWANDA. Kareba, versant sud du Karisimbi, [−1.5518°; 29.4536°], elev., 3050 m, 10/X/1974, *P. Auquier 4509* (FI-PS).

9. ***Hypolepis rugosula*** subsp. ***africana*** (C. Chr.) Schwartsb. & J. Prado. Lectotype: **MADAGASCAR.** Süd-Betsiléo, Wald von Ankafina, [−18.3819°; 48.0996°], III/1881, *J.M. Hildebrandt 4139* (B! [20 0075279]; isolectotypes: B! [20 0075278], B! [20 0075283], BM!, LE!, LE! [ex Herb. Petropol.], P-*n.v.*-2 sheets, G! [ex Herb de Candolle], G!-on 2 sheets [ex Herb. Barbey-Boissier], W!).
? *Phegopteris boryana* Mett. Syntypes?: **MAURITIUS.** [−20.2906°; 57.5870°], 1846-1848, *Boivin s.n.* (W! [133/78-29], W! [133/78-30]); **BOURBON.** s.d., *Bory s.n.* (RB!-frag. [215817]).

Specimens examined: **MADAGASCAR.** Tanala, [−20.9505°; 44.8154°], s.d., *L. Kitching s.n.* (K!—syntype of *H. rugosula* var. *africana*); Pic d'Ivohibe, [−22.5122°; 46.9671°], s.d., *Humbert 3324* (BM!, C-*n.v.*, P-*n.v.*-3 sheets—syntypes of *Hypolepis rugosula* var. *africana*).
REUNION ISLAND [ILE BOURBON]. [−21.1231°; 55.5278°], 1836, *A. DeLessert s.n.* (G-on 2 sheets); [−21.2256°; 55.6074°], 1853, *Boivin B 813* (FI, G-2 sheets); s.d., *Richard 494* (FI-W, LE); s.d., *J. de Cordemoy 41* (K); s.d., *L.J. Grey s.n.* (K); s.d., *I.B. Balfour s.n.* (K); s.d., *de Montbrisón s.n.* (RB [13288]); Plaine des Fougéres, 1850, *Anonymous* (K [ex Herb. Mus. Paris]); s.d., *Anonymous* (OXF); s.d., *Anonymous* (K [ex Herb. Mus. Paris]).

10. ***Hypolepis rugosula*** subsp. ***rudis*** (Kunze) Schwartsb. Lectotype (designated here): **PHILIPPINES. [Luzon]:** in Philippinis, [Prov. Albay], [16.5394°; 121.3921°], [1841], *H. Cuming 140* (B! [20 0075269]; isolectotypes: B! [ex Herb. Koenpreuss], FI-W!, G! [ex Herb. Moricand], K**!** [000492488] K! [000 492495], LE! [ex Herb. Fischer], LE! [ex Herb. Petropol.], OXF!, RB!, W! [ex Herb. Mus. Wien], W! [ex Herb. Palat. Vindob]).

Specimens examined: **PHILIPPINES. Central Luzon:** Prov. Bataam, Mt. Mariveles, Lamao R., 14°32'N; 120°29'E, elev., 350 ft, 05/XII/1903, *R.S. Williams 294* (K).

11. ***Hypolepis rugosula*** subsp. ***archboldii*** (Copel.) Schwartsb. Type: **[NEW GUINEA].** [Dutch New Guinea, Mt. Wilhelmina, 7 km northeast of Wilhelmina-top, elev., 3560 m, subalpine forest, common in ground moss, IX/1938], [−4.2185°; 138.8669°], *L.J. Brass & E. Meyer-Drees 9852* (holotype: MICH-*n.v.*; isotypes: BM-*n.v.*, FI-PS!, L! [0051755], UC [image!]).

12. ***Hypolepis rugosula*** (Labill.) J. Sm. subsp. ***rugosula*.** Lectotype: **[TASMANIA].** Habitat in Capite Van-Diemen, [1791-1793], *Labillardière s.n.* (FI-W!-214897; isolectotypes: FI-W!-214898, FI-W!-214899, FI-W!-on 2 sheets [214903, 214904], FI-W!-216239, FI-W!-218473, G!-on 2 sheets [00048249, 00048250], G!-on 2 sheets [00048252, 00048253], G!-00048255, LE!-2 sheets; probable isolectotypes: B! [ex Herb. Mertens], G!-00048251, K!, L!- 908837-403, PRC!).

Cheilanthes amaurorachis Kunze. Lectotype: **[TASMANIA].** Cultis Hortis Lipsiae ex Tasmania, s.d., *Anonymous s.n.* [*G. Kunze*?] (B! [20 0074521]; possible isolectotypes: BR!, K! [ex Herb. Hooker], K! [ex Herb. Kew]).

Hypolepis australis N.A. Wakef. Type: **AUSTRALIA. Eastern Victoria:** Arte River, [−37.5430°; 148.7890°], 23/III/1941, *N.A. Wakefield 107* (holotype: MEL-*n.v.* [1512588]).

Specimens examined: **AUSTRALIA. Queensland:** Brisbane, [−27.4747°; 153.0218°], s.d., *A. Dietrich s.n.* (LE *p.p.* [labeled "1" by Schwartsburd]); Lamington National Park, [−28.1926°; 153.1218°], elev., ca. 1000 m, 13/V/1977, *B.S. Parris & J.P. Croxal 6235* (K). **New South Wales:** The Gulf Creek, sunny corner, 15 miles east-north-east of Bathurst, [−33.3745°; 149.6600°], 03/III/1964, *E.F. Constable 4759* (K); Mt. Spirabo, 20 miles SSE of Tenterfield, [−29.2670°; 152.1081°], elev., 1440 m, 07/V/1961, *E.F. Constable NSW P8321* (K-on 5 sheets); The Wines, south of Sassafras, [−35.0509°; 150.2612°], 19/X/1957, *E.F. Constable NSW P7957* (K); below Govetts Leap, Blackheath, 33°38'S; 150°19'E, elev., 660 m, 15/III/1977, *R. Coveny & S.K. Roy 9190* (K, WELT). **Australian Capital Territory:** New Chum Road, Cotter Valley, [−35.6088°; 148.8236°], 30/III/1964, *M. Gray 7423* (MBM-on 3 sheets). **Victoria:** Dandenong Ranges, [−37.9417°; 145.2900°], s.d., *J.G. Luchmann s.n.* (UPS [499351]); Peninsula Country Golf Club, near Franstone, 40 km south-south-west of Melbourne, 38°08'S; 145°11'W, 07/X/1973, *R.J. Chinnock P781* (K-on 3 sheets); East Gippsland, [−38.3680°; 146.6118°], 10/II/1973, *A.C. "Beanglehole" 41430* (K); Dematis Gully, 11/V/1953, *R. Melville & J. Willis 3842* (K). **Unknown locality:** s.d., *F. von Mueller s.n.* (BR); Jenolan Caves, X/1899, *W.F. Blakely s.n.* (FI).

KANGAROO ISLAND [AUSTRALIA, South Australia]. ca. 4 km east of Cape Borda, [−35.8109°; 137.1885°], 29/XII/1957, *R. Schodde 528* (K-on 2 sheets).

KING'S ISLAND [TASMANIA, King's Island]. 1802-1805, [−39.8581°; 143.9852°], *R. Brown 16a* (K, LE).

TASMANIA [VAN DIEMEN'S LAND]. [−41.4882°; 145.7309°], 1831, *Lawrence s.n.* (K); [−41.4186°; 147.7167°], 1833, *R.C. Gunn s.n.* (BR); s.d., *R.C. Gunn s.n.* (FI, LE-2 sheets); 31/VIII/1840, *J.D. Hooker 1275* (K); 1843, *S.G. Hannaford s.n.* (G-on 2 sheets); Valley Mount Wellington, [−42.8958°; 147.2652°], 1820?, *A. Wossman s.n.* (FI-W [214907]); Gordon River road, E of Wedge River, ca. 44 km W of Maydena, 42°43.3'S; 146°16.3'E, 05/XII/2007, *P.J. Brownsey PJB TAS 29* (WELT-on 2 sheets); s.d., *W. Archer s.n.* (LE); 1861?, *Anonymous* (OXF); s.d., *Anonymous* (W).

13. ***Hypolepis rugosula*** subsp. ***lactea*** (Bronswey & Chinnock) Schwartsb. Type: **NEW ZEALAND. Wellington:** Eastbourne, Butterfly Creek, around fallen log, disturbed ground on creek bank, in beech forest, [41°18'S; 174°54'E], 21/II/1979, *P.J. Brownsey NZ 1356* (holotype: WELT! [P11516a]; isotype: CHR-*n.v.*).

Specimens examined: **NEW ZEALAND, NORTH ISLAND.** South Auckland, Kauaeranga Valley, [−36.9520°; 174.4936°], elev., 500 ft, 30/I/1971, *J.P. Croxall & B.S. Parris 1479* (K-on 2 sheets); Rodney County, Kaipara Hills, 36°25'S; 174°30'E, elev., 140 m, 04/I/1987, *M.E. Young s.n.* (WELT-on 3 sheets [P 17888 a-c]); Wellington, Mt. Kaukau, [−41.2343°; 174.7805°], elev., 1500 ft, VIII/1971, *R.J. Chinnock & B.S. Parris 3172* (K-on 2 sheets); Wellington Prov., east of Masterton, Stronvar, Te Haroto Station, 41°04'S; 175°56'E, elev., 300 m, 12/III/2008, *P.J. Bronwsey s.n.* (WELT [P 022219]); Wellington Prov., east of Masterton, Stronvar, Te Haroto Station, 41°04.3'S; 175°56.3'E, elev., 300 m, 12/III/2008, *B. Sneddon & L. Perri s.n.* (WELT [P 022218]).

NEW ZEALAND, [WAIKATO], MIDDLE ISLAND. [−36.9574°; 176.0804°], s.d., *Strange s.n.* (LE *p.p.*).

NEW ZEALAND, SOUTH ISLAND. Greymouth, [−42.4612°; 171.2266°], 1875-1885, *R. Helms*, *N.Z.E. 49 p.p.* (L-384114); Greymouth, VI/1879, *R. Helms s.n.* (PR); Fiordland, Milford Sound, [44°37'S; 167°52'E], 11/XII/1989, *J.C. Smith-Dodsworth s.n.* (WELT-on 2 sheets [P 18047a and P 18047b]).

NEW ZEALAND. Unknown locality: 1843-1844, *W. Stephenson 21* (G-2 sheets, K, W); Port Nicholson, V/1849, *D. Lyale s.n.* (K); s.d., *Knight s.n.* (RB [215825 A]).

14. ***Hypolepis rugosula*** subsp. ***rufobarbata*** (Colenso) Schwartsb. Lectotype: **NEW ZEALAND.** Waipawa County, between Norsewood and Danneverke, hills, skirts woods, [−39.9000°; 176.5892°], 1882, *W. Colenso s.n.* (WELT! [P3346]; isolectotype: K!).

Polypodium viscidum Colenso. Lectotype: **NEW ZEALAND.** open spots, mountains, near Waikare Lake, [−37.4299°; 175.2652°], XII/1841, *W. Colenso s.n.* (WELT-*n.v.* [P3189]; probable isolectotype: K! ["*Colenso 269*"]).

Specimens examined: **NEW ZEALAND, NORTH ISLAND.** Auckland, 1859, *F. Hochstetter 36* (W-2 sheets); Auckland, Spragg's Bush, Waitakere Ranges, [−36.8652°; 174.5178°], 19/IX/1970, *B.S. Parris 853* (K); South Auckland, Mt. Pirongia, 23/IV/1966, *J.J. Bedford s.n.*, *Exsic. Parris 514* (K-on 2 sheets); South Auckland, Kaitarakihi track from Kopu-Hikuai road, [−37.0384°; 175.2042°], elev., 2000 ft, 31/I/1971, *B.S. Parris & J.P. Croxall 1480* (K); South Aukland, Mt. Te Aroha, [−37.5346°; 175.7430°], elev., 2700 ft, 09/I/1971, *B.S. Parris & J.P. Croxall 1453* (K); Taxod forest at Ohakune, Tongariro National Park, [−39.0334°; 175.7545°], 06/X/1929, *W.A. Sledge 169* (K); Taupo Co., 38°57'S; [176.0733°], elev., ca. 1180 ft, 01/XII/1983, *R.O. Gardner 4009* (K); Te Aroha, Tawa-Rata forest, elev., 1600 ft, 15/I/1966, *B.S. Parris 334* (K); Kaukau, Howraki Gulf, [−41.2294°; 174.7826°], XII/1848, *Lyell s.n.* (K-2 sheets); Taranaki, Mt. Egmont National Park, [−39.2963°; 174.0640°], elev., 2800 m, 15/IV/1966, *B.S. Parris 475* (K); Taranaki, Mt. Egmont, Stratford road, 26/X/1970, *B.S. Parris 1024* (K); Kaitoke Waterworks, Upper Hut, [−41.1382°; 175.1525°], 20/II/1979, *P.J. Brownsey NZ 1359* (WELT-on 2 sheets); (from) Murgaroa Swamp, Upper Hut, (cultivated at Orari Gardens, Wellington), 20/XII/1979, *P.J. Brownsey NZ 1435* (WELT); Wellington, Mt. Kaukau, elev., 1500 ft, VIII/1971, *R.J. Chinnock & B.S. Parris 3173* (K); Wellington, Pihanga Saddle, 15/VIII/1970, *J.P. Croxall & B.S. Parris 769* (K); Wellington, Akatarawa Saddle, [−40.9905°; 175.1417°], elev., 1400 ft, 23/X/1970, *B.S. Parris 954* (K); Grey Co., North of Barrytown, 42°12'S; [171.4622°], *R.O. Gardner 4492* (K).
NEW ZEALAND, [WAIKATO], MIDDLE ISLAND. [−36.9563°; 176.0850°], s.d., *Strange s.n.* (LE *p.p.*).
NEW ZEALAND, SOUTH ISLAND. Westland, Valley of the Teremakau, [−43.4443°; 170.0981°], 1889, *T.B. Cartwright s.n.* (OXF); Westland, foresta all'inizio del sentiero per il Fox Glacier dove si abbandona la strada, versante destro de la valle, [−43.4763°; 170.0435°], 10/XI/1956, *R.E.G. Pichi-Sermolli 6276* (FI-PS); Canterbury, sulle rive del torrente dell'Ashley Gorge nella foresta di *Nothofagus cliffortioides*, [−43.5651°; 170.8556°], 10/XI/1956, *R.E.G. Pichi-Sermolli 6192* (FI-PS); Greymouth, [−42.6642°; 171.4964°], VIII/1878, *R. Helms s.n.* (G); Greymouth, s.d., *R. Helms s.n.* (PRC); Greymouth, 1875-1885, *R. Helms*, *N.Z.E. 49 p.p.* (L-384113); Otira, Westland, Barrack Creek banks, [−42.8316°; 171.5804°], elev., 1700 ft, *N. Lothian s.n.* (K); Canterbury, Banks Peninsula, Kaituna Valley below Herbert Peak, 28/XII/1961, *R. Melville 5775* (K-on 2 sheets); Dunedin, [−45.7766°; 170.4040°], I-IV/1875, *M. Filhol s.n.* (LE).
NEW ZEALAND, STEWART ISLAND. [−46.8836°; 167.9295°], II/1910, *B. Leland et al. 317* (G, K).
NEW ZEALAND. Unknown locality: [Middle Island?], 1850?, *Strange s.n.* (G-on 2 sheets); 1875, *W. Walker s.n.* (FI); 1881, *W. Colenso s.n.* (K); s.d., *W.T.L. Travers s.n.* (LE *p.p.*); s.d., *Knight s.n.* (RB [215825 B]).

15. ***Hypolepis rugosula*** subsp. ***subantarctica*** (Bronswey & Chinnock) Schwartsb. Type: **[NEW ZEALAND, CAMPBELL ISLAND].** Cultivated at CHR (G 11407) from Campbell Island, *ex D.R. Given s.n.*, 26/III/1981, *P.J. Brownsey s.n.* (holotype: WELT!-on 2 sheets [P11518/A and P11518/B]; isotypes: AK-*n.v.*, CHR-*n.v.*).

Specimens examined: **NEW ZEALAND, CAMPBELL ISLAND.** Above Smoothwater Bay, [−52.5409°; 169.1804°], 23/III/1947, *W.B. Brockie s.n.* (WELT [P 7786]).