Acta Societatis Botanicorum Poloniae

Article ID: 8936
DOI: 10.5586/asbp.8936

**Publication History**
Received: 2020-06-30
Accepted: 2020-07-15
Published: 2020-11-20

**Handling Editor**
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**Authors' Contributions**
RO conceived and performed the taxonomic research and wrote the manuscript; VP prepared the figures, consulted the research, and edited the manuscript

**Funding**
The work was financed through the statutory fund of the W. Szafer Institute of Botany, Polish Academy of Sciences, the EU structural funding Operational Programme Research and Development for Innovation (project No. CZ.1.05/2.1.00/19.0388), and the Ministry of Education, Youth and Sports of the Czech Republic in the "National feasibility program I" (projects LO1208 "TEWEP" and SGS12/PřF/2020).

**Competing Interests**
No competing interests have been declared.

**ORIGINAL RESEARCH PAPER in RECENT DEVELOPMENTS IN TAXONOMY AND PHYLOGENY OF PLANTS**

# The Sinking of Another Tristan da Cunha Moss Endemic and Its Phytogeographical Consequences

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## Abstract

The original material of *Isopterygium tristaniense* Dixon, an endemic species of the Tristan da Cunha archipelago in the central South Atlantic Ocean, is taxonomically evaluated and some details of its morphology are illustrated. The species is found to be conspecific with the Holarctic *Pseudotaxiphyllum elegans* (Brid.) Z. Iwats. and this is the third record of the species in the Southern Hemisphere. The global distribution of this species is reviewed, and the distribution patterns of the South Atlantic mosses are briefly discussed.

## Keywords

Afro-American disjuncts; amphi-Atlantic distribution; Bryophyta; Musci; phytogeography; Atlantic Ocean; southern cool-temperate zone; taxonomy

## 1. Introduction

Tristan da Cunha is the largest island of a small volcanic archipelago in the central South Atlantic Ocean, which lies approximately mid-way between the southern end of South Africa and southern South America and consists of two island groups. The northern group comprises three main islands close to one another, Tristan da Cunha, Inaccessible Island, and Nightingale Island, and a few outlying islets and rocks, located at 37°02′–37°24′ S and 12°12′–12°42′ W. The southern group contains only the orphaned Gough Island and about a dozen or so islets and rocks lying 370 km south-south-west of Tristan da Cunha at 40°19′ S and 9°57′ W. The archipelago is highly isolated, and its remoteness is best illustrated by the distances to the conterminous continents, which are, roughly, 2,400 km to South Africa, 3,000 km to South America, and 3,200 km to Antarctica. The islands are the summits of massive shield volcanoes of Tertiary origin and their age varies from 18 million years (Nightingale Island) to 0.5 million years (Tristan da Cunha) (Ollier, 1984; Preece et al., 1986). They are situated just north of the Subtropical Convergence in the south-cool-temperate zone and experience a cool, humid, oceanic climate with a mean annual temperature of 15 °C, precipitation of 1,700 mm/year, prevalent westerly winds, and often heavy cloud cover (Höflich, 1984). Their vegetation cover consists of tussock grassland, fern bush, wet heath, moorland, feldmark, and peat bogs (Wace, 1961).

Although the Tristan da Cunha archipelago was discovered at the very beginning of the sixteenth century in 1505 (Gough Island) and 1506 (Tristan da Cunha group) (Headland, 1989; Wace, 1969), the first botanical collection, including bryophytes, was made only on January 3–7, 1793 (Du Petit-Thouars, 1808, 1811). In the nineteenth century, only two small collections were made in the northern group of the archipelago by the British expeditions of H.M.S. Herald in 1852–1854 and H.M.S. Challenger in 1872–1876 (Mitten, 1875, 1876, 1884). Likewise, in the first half of the twentieth century, small collections of mosses were made in the northern group of islands by the Norwegian Antarctic expedition in 1927–1928 and the British naval voyage of H.M.S. Carlisle in 1937 (Dixon, 1937, 1939). The composite survey of the northern group made by the Norwegian scientific expedition to Tristan da Cunha of 1937–1938 was much more successful; it provided, among others, a substantial collection of mosses. They were studied by H. N. Dixon and the results were posthumously published in the most comprehensive treatment of mosses in the Tristan da Cunha group (Dixon, 1960). Finally, a large collection of bryophytes from Tristan da Cunha by the Royal Society Expedition in 1962 made a comprehensive examination of the islands following the volcanic eruption in 1961 (Dickson, 1965; Wace & Dickson, 1965).

Altogether, during over 150 years of bryological exploration up to 1965, approximately 130 species of moss have been recorded from the Tristan da Cunha group, 59 of which are endemic. Since then, four more species have been added to the moss flora of this area, including *Hygrodicranum falklandicum* Cardot (Blockeel et al., 2007), *Bucklandiella striatipila* (Cardot) Bedn.-Ochyra & Ochyra (Bednarek-Ochyra & Ochyra, 2013; Ochyra et al., 2015), *B. sudetica* (Funck) Bedn.-Ochyra & Ochyra (Ellis et al., 2019), and *B. pachydictyon* (Cardot) Bedn.-Ochyra & Ochyra (Ellis, Alegro, et al., 2015); however, the real number of species cannot be precisely established because many species recorded from this area still need critical reassessment. A reexamination of the voucher specimens of some species reported from the Tristan da Cunha group revealed them to be species reported from this area under different names, resulting in the reduction of the total number of species in the archipelago. For instance, the material named *Barbula validinervia* Müll. Hal. represents *Ceratodon purpureus* (Hedw.) Brid. (Ochyra, 1999a), *Grimmia kerguelensis* Cardot is *Guembelia kidderi* (James) Ochyra & Żarnowiec (Ochyra & Hertel, 1990), *Racomitrium nigritum* (Müll. Hal.) A. Jaeger and *R. subnigritum* (Müll. Hal.) Paris are *Bucklandiella lamprocarpa* (Müll. Hal.) Bedn.-Ochyra & Ochyra (Bednarek-Ochyra, 2014c, 2015; Bednarek-Ochyra et al., 1996; Bednarek-Ochyra & Ochyra, 2012b; Ochyra et al., 1988; Ochyra & Van Rooy, 2013), and *Didymodon austroalpigenus* (Müll. Hal.) Broth. is *Bryoerythrophyllum campylocarpum* (Müll. Hal.) H. A. Crum (Ellis, Aranda, et al., 2013).

The true level of endemicity in the Tristan da Cunha group is apparently much lower and of the many putative endemic species from this area which have hitherto been taxonomically assessed, the status of a distinct species was confirmed only for *Blindia brachystegia* Dixon (Bartlett & Vitt, 1986). The examination of numerous other species described from this area revealed their conspecificity with species discovered earlier in adjacent territories. For example, *Bryum cymbifoliellum* Dixon is *Plagiobryoides orbiculatifolium* (Cardot & Broth.) Ochyra & Bedn.-Ochyra (Ochi, 1972; Ochyra & Singh, 2008), *Hypnum elatum* Dixon is *H. chrysogaster* Müll. Hal. (Ando, 1972, 1976), *Thuidium curvatum* Mitt. is *Th. furfurosum* (Hook. f. & Wilson) Reichardt (Touw & Falter-van den Haak, 1989), *Rigodium crassinervium* E. B. Bartram is *Kindbergia praelonga* (Hedw.) Ochyra (Zomlefer & Buck, 1990), *Racomitrium breutelioides* Dixon is *Dilutineuron laevigatum* (Mitt.) Bedn.-Ochyra et al. (Bednarek-Ochyra & Ochyra, 1992), *Dichodontium opacifolium* Dixon is *Chrysoblastella chilensis* (Mont.) Reimers (Ochyra, 1999b; Sollman, 1999), and *Ditrichum tenuinerve* Dixon is *Blindia robusta* Hampe (Bednarek-Ochyra, 2014a). These changes do not affect the diversity statistics of the moss flora because they refer only to the changes in the names of the otherwise accepted distinct species. *Isopterygium tristaniense* Dixon also belongs to this category of species and its case is discussed herein.

## 2. Results

### 2.1. The Type Material of *Isopterygium tristaniense* and Its Identity

*Isopterygium tristaniense* was described by Dixon (1960) on the basis of two specimens collected in 1938 by Erling Christophersen, the leader of the Norwegian scientific expedition to Tristan da Cunha in 1937–1938. One of these specimens was recorded on Tristan da Cunha on rock at an elevation of 800 m and was designated as the type, whereas the second specimen was also gathered from rock at an altitude of 275–300 m and is automatically the paratype.

The original material of *Isopteygium tristaniense* consists of rather small, fairly rigid plants, in thin, lustrous and rather loose, dark green to yellowish or yellow-green mats. The stems are short, 1.0–1.5 cm long and 1.3–1.5 mm wide including the leaves, procumbent, complanate-foliate, simple or sparsely, irregularly and freely branched (Figure 1A), with clusters of smooth, brown, sparingly branched rhizoids below leaf insertions, in transverse sections rounded with one–two rows of small to medium-sized, 10–15 µm wide, brown, firm-walled cortical cells surrounding two–three rows of large, colorless, thin-walled medullary cells, without a hyalodermis and central strand. The pseudoparaphyllia are absent. The axillary hairs are infrequent, filiform, and consist of a short, light brown basal cell and two–three elongate, hyaline distal cells. The stem and branch leaves are similar in shape, somewhat rigid to semi-flaccid, close to somewhat distant, erect-spreading when dry, hardly altered on wetting, flat to somewhat concave, nondecurrent, (1.0–)1.4–1.8 mm long, (0.3–)0.4–0.55 mm wide, symmetric to slightly arcuate, acuminate to a filiform, and acute apex (Figure 1B–E). The leaf margins are plane to erect all around, serrated at the apex (Figure 1F), and serrulate to entire below (Figure 1G–I). The costa is weak and indistinct to fairly strong, short and double, with one branch extending to one third way up the leaf. The mid-leaf and distal cells (Figure 1F–H) are linear-fusiform to linear, often flexuose, gradually tapering towards the ends, thin-walled, 70–140(–160) µm long, 5–7 µm wide, and becoming shorter towards the base. The alar cells (Figure 1I) are undifferentiated or consist of one–four quadrate to short-rectangular cells at the basal angles. The plants are dioicous, but only male plants with a few perigonia were found. No sporophytes and propagules are present.

In a short taxonomic discussion, Dixon (1960) stated that the specimen No. 2193 (paratype) from Nightingale is "a larger plant, with more complanate, broader, somewhat arcuate leaves." Actually, slightly asymmetric leaves are mixed with symmetric ones on the same shoots and the larger stature of the plant is not a critical point which should give rise to any problems of identification. A careful comparison of the leaves of the two specimens cited in the protologue additionally revealed that the type specimen (No. 1377) has leaf margins strongly serrated at the leaf apex and weakly serrated to the leaf middle, whereas in the paratype specimen (No. 2193) the leaf margins are strongly serrated near to the base, but the extent of the serrulation of the leaf margins is variable. Despite these differences between the two specimens cited in the protologue, they clearly represent the same species, which shows some variability in the leaf shape and the serrulation of the leaf margins.

Additionally, Dixon (1960) stated that the new species is "perhaps nearest to *I.*[*sopterygium*] *fuegianum* Besch., but that is autoicous, with narrower leaves and the habit of *I. pulchellum*, which the present plant does not at all suggest." This statement is entirely true because these two species actually have nothing to do with each other. *Isopterygium fuegianum* is easily differentiated by having a stem with a somewhat indistinct hyalodermis of small and thicker-walled cells, coupled with the lack of pseudoparaphyllia, entire or sometimes minutely serrulate leaf margins and papillose rhizoids in the leaf axils. This combination of characters immediately excludes this species from *Isopterygium* Mitt. and places it in *Isopterygiopsis* Z. Iwats., a segregate of the broadly conceived genus *Isopterygium* (Iwatsuki, 1970, 1987). In fact, *Isopterygium fuegianum* is conspecific with *Isopterygiopsis pulchella* (Hedw.) Z. Iwats. (Ireland & Buck, 2009; van Zanten, 1971), a bipolar species extending to New Zealand and polar regions in the Southern Hemisphere (Ochyra, Bednarek-Ochyra, & Lewis Smith, 2002; Ochyra, Lewis Smith, & Bednarek-Ochyra, 2008).

The only trait that *Isopterygiopsis pulchella* shares with *Isopterygium tristaniense* is a lack of pseudoparaphyllia, which excludes it from the genus *Isopterygium* (in which filamentous pseudoparaphyllia are present). In contrast, pseudoparaphyllia are absent in the genus *Pseudotaxiphyllum* Z. Iwats., another segregate of *Isopterygium* (Iwatsuki, 1987) distinguished by the lack of hyalodermis and the presence of small and thick-walled cortical stem cells, smooth rhizoids below the leaf insertions,

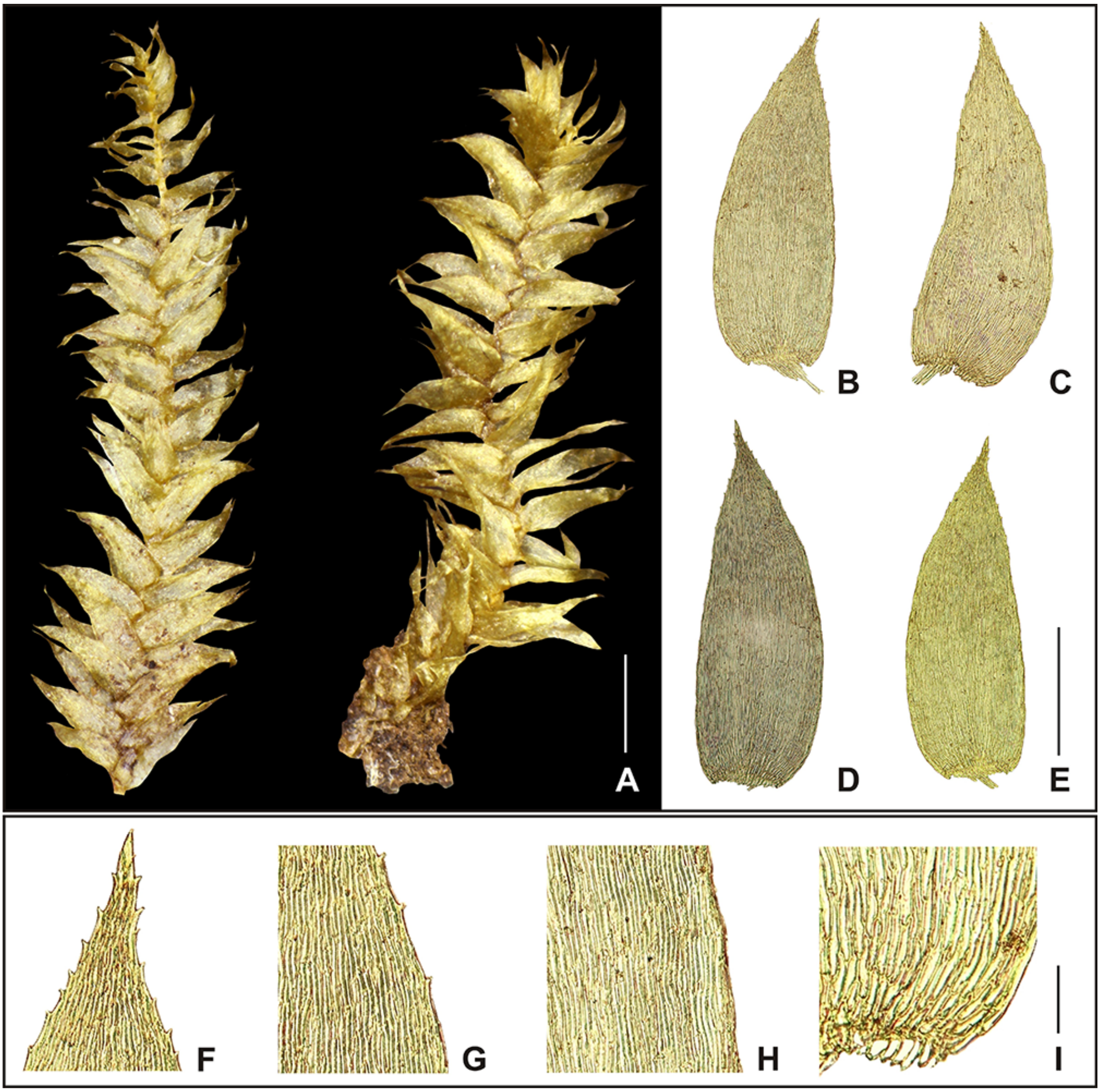

**Figure 1** *Pseudotaxiphyllum elegans*. (**A**) Habit. (**B–E**) Leaves. (**F**) Leaf apex. (**G**) Distal leaf cells and margin. (**H**) Mid-leaf cells and margin. (**I**) Basal and angular leaf cells. **A–C** and **F–I** from Christophersen 2193 (FH-Bartram, paratype of *Isopterygium tristaniense*), **D–E** from Christophersen 1377 (FH-Bartram, lectotype of *Isopterygium tristaniense*). Scale bars: (**A**) 1 mm; (**B–E**) 0.5 mm; (**F–I**) 100 µm.

serrate to serrulate leaf margins, occasional presence of asexual reproductive brood bodies, and a mostly dioicous sex condition. This combination of characters is, except for the lack of vegetative propagules, present in *Isopterygium tristaniense*, for which *Pseudotaxiphyllum* appears to be the proper home.

*Pseudotaxiphyllum* is a small genus of pleurocarpous mosses comprising some 12 species (Crosby et al., 2000; Iwatsuki & Tan, 2004; Li et al., 2015). Of these, 11 species occur in the Holarctic; only *P. falcifolium* (Hook. f. & Wilson) S. He is endemic to New Zealand (Gibb et al., 2018). Two of these species deeply penetrate the tropics or the Southern Hemisphere: *P. distichaceum* (Mitt.) Z. Iwats., which extends to montane outposts in Central America (Allen, 2018), northern South America, southeastern Brazil (Ireland & Buck, 2009), St. Helena in the South Atlantic Ocean (Ellis et al., 2017), and Réunion Island in the Mascarene Islands in the South Indian Ocean (Arts, 2005); and *P. elegans* (Brid.) Z. Iwats. which has been recorded on the Hawaiian Islands (Hoe, 1979) and in southern South America (Ireland & Buck, 2009). These two species are well known by the frequent presence of asexual reproductive bodies. In the first species, the propagules are clustered at the stem apices and upper leaf axils and they are twisted linear-vermiform with one–five peg-like leaf primordia at their apices. In the latter species, the brood bodies are usually clumped in the leaf axils below the stem apices and look like miniature parental plants bearing well-spaced, reduced leaves throughout.

Unfortunately, the brood bodies are not always present in these species and, for example, they are entirely missing in the Mexican plants of *Pseudotaxiphyllum distichaceum* (Ireland, 1994), and are best distinguished by the asymmetric and often cultriform leaves. In contrast, the leaves of *P. elegans* are usually symmetric or only slightly asymmetric and arcuate, but never cultriform. In general, *P. elegans* exhibits a remarkable phenotypic plasticity, especially with regard to the stature of the plants and leaf shapes. Consequently, its various phenotypes were often recognized taxonomically as distinct varieties, but detailed morphological studies of the leaves in the Belgian populations of this species showed that these varieties should not be maintained as distinct taxa (Lefebvre, 1963). A similar conclusion was presented by Ireland (1969); after a thorough study of the species over its whole geographical range, they found that neither variety of *P. elegans* seems worthy of taxonomic recognition because the size and leaf curvature are very variable and do not correlate with other characters.

*Pseudotaxiphyllum elegans* is recognized by its leaves that are close to somewhat distant, erect-spreading, lanceolate to oblong-lanceolate and acuminate with serrulate to strongly serrate leaf margins above, and serrulate to entire below. In addition, it has narrow mid-leaf cells and not or poorly differentiated alar cells. All of these features occur in plants of *Isopterygium tristaniense*, and although they entirely lack any reproductive asexual propagules, its leaves perfectly match those of *P. elegans*, and therefore these species are here considered conspecific.

### 2.2. Taxonomic and Nomenclatural Conclusion

***Pseudotaxiphyllum elegans*** (Brid.) Z. Iwats., J. Hattori Bot. Lab. 63: 449. 1987.

*Isopterygium tristaniense* Dixon, *Results Norweg. Sci. Exped. Tristan da Cunha* 48: 45. 1960. **Type citation:** Tristan da Cunha: On rock, Hottentot Gulch, 800 m., No. 1377, type. Nightingale: Sheltered rock at Peak, 275–300 m., No. 2193. **Lectotype** (designated here): "Tristan da Cunha Norwegian Scientific Expedition 1937–1938 Isopterygium tristaniense Dix. By Hottentot Gulch, on rock, 800 m Tristan da Cunha: 28 Jan. 1938 leg. E. Christophersen No. 1377 det. H. N. Dixon" – FH-Bartram 213423! **Paratype:** "Tristan da Cunha Norwegian Scientific Expedition 1937–1938 Isopterygium tristaniense Dix. at Peak, rock, sheltered 275–300 m Tristan da Cunha Nightingale: 10 Feb. 1938 leg. E. Christophersen No. 2193 det. H. N. Dixon" – FH-Bartram 290232! **syn. nov.**

Despite sinking the next endemic species of the Tristan da Cunha group, the genus *Isopterygium* has not been excluded from the moss flora of this area. This is because *I. ambiguum* Cardot, another species of this genus reported from this archipelago, proved to be conspecific with *I. tenerifolium* Mitt. (Ochyra & Plášek, 2019), an Afro-American species, widespread in the Neotropics and once found in the Cape in South Africa (Ochyra & Ireland, 2016). In addition, there is another species of this genus, *I. brownii* Cardot, known from Gough Island in the southern group of the archipelago (Cardot, 1911, 1912). This species has not hitherto been taxonomically assessed, and a preliminary study suggests that it is a distinct species. The type material of this species requires a thorough comparison with numerous African species of *Isopterygium*, many of which have not been critically assessed since their description.

## 3. Discussion

The discovery of *Pseudotaxiphyllum elegans* in the Tristan da Cunha group represents a major geographical range extension of this species and confirms its status as a bipolar species with transitional localities at lower latitudes. It is principally a panholarctic species, having a strongly dissected suboceanic boreo-temperate range in the Northern Hemisphere. It is widespread and locally common in Western Europe, extending from Iceland and northern Fennoscandia to southern Portugal and the Mediterranean (Ros et al., 2013), and is becoming progressively rare to the east, where it reaches Karelia (Abramov & Volkova, 1998) and Leningrad Province (Afonina, 2004) in northwestern Russia, the Ukraine (Bachuryna & Mel′nychuk, 2003) and Romania (Mohan, 1998), some isolated stations in Georgia and the Caucasus (Ignatov et al., 2006), and in the coastal areas of the central Black Sea in Turkey (Erdağ & Kürschner, 2017). In Asia, the species is very rare in the Russian Far East, including Chukotka, Kamchatka, and Southern Primorye (Afonina, 2004; Cherniad′′eva, 2012). Finally, in North America, *P. elegans* is bicentric in its distribution (Ireland, 1969, 2014). In the western part of the continent, it extends from southwestern Alaska and the Yukon through British Columbia to California (Norris & Shevock, 2004). In eastern North America, it is distributed from Newfoundland, Labrador, Québec, and Ontario to Georgia and Alabama in the south, and Minnesota, Missouri, and Arkansas in the west.

Outside the Holarctic, apart from the present discovery in the Tristan da Cunha group at approximately lat. 37° S, *Pseudotaxiphyllum elegans* is known in two regions. As is the case with many northern species, it deeply penetrates into the tropics and it is known to exist on altimontane outposts on the island of Maui in the Hawaiian Islands archipelago in the Pacific Ocean (Hoe, 1979). Moreover, it is known to occur in southern South America in the Southern Hemisphere where it was once recorded in Bío-Bío Province in south Chile at lat. 38°28′ S and on West Falkland in the Falkland Islands at lat. approximately 51°30′ S (Cardot & Brotherus, 1923; Ireland & Buck, 2009). Thus, the latter discovery makes *P. elegans* a typical broadly defined bipolar species, with some intermediate occurrences at lower latitudes.

The problem of bipolar bryophyte species is one of the most interesting – and most discussed – biogeographic phenomena. Since the formulation of a classic and fairly broad definition of bipolar plant species (Du Rietz, 1926, 1940), this issue has attracted the attention of many bryologists (e.g., Ochyra, 1992; Ochyra & Buck, 2003; Schofield & Crum, 1972; Schofield, 1974; Schuster, 1983) who overviewed it and proposed various, more or less critical, lists of bipolar bryophyte species. There are basically two distinct categories of bipolar disjuncts: strict bipolar species and transitional bipolar species. Species of the former category occur exclusively in cold and temperate regions of both hemispheres without any transitional occurrences in tropical regions, whereas those belonging to the latter category have intermediate localities in high mountains in the tropics (Ochyra, Lewis Smith, & Bednarek-Ochyra, 2008). The lists of bipolar species themselves are constantly changing; exploration of poorly studied areas constantly yields new floristic finds and taxonomic studies often lead to changes in the biogeographic statuses of many species.

The taxonomic circumscription of some bipolar species is still poorly understood, and, in some cases, molecular data has proven to be useful in making a final decision regarding their taxonomic status. The most spectacular example is the discovery that *Sphagnum magellanicum* Brid., one of the most common species of peat moss in the Northern Hemisphere, is actually a narrow endemic of southern South America because the northern plants were proven to represent two distinct species, *S. medium* Limpr. and *S. divinum* Flatberg & K. Hassel (Hassel et al., 2018). *Didymodon brachyphyllus* (Sull.) R. H. Zander was considered to be a bipolar species when its conspecificity with the Antarctic *D. gelidus* Cardot and *Barbula byrdii* E. B. Bartram was shown (Ochyra & Zander, 2002; Zander & Ochyra, 2001); however, reexamination of these taxa revealed a definite distinctness of northern and southern species both on morphological (Jiménez & Ochyra, 2017) and molecular grounds (Ronikier et al., 2018). The South American and sub-Antarctic *Drepanocladus longifolius* (Mitt.) Paris (Li et al., 2009; Ochyra, 1989; Ochyra & Matteri, 2001; Ochyra, Bednarek-Ochyra, & Lewis Smith, 2008 ) was considered identical to the panholarctic *D. capillifolius* (Warnst.) Warnst. (Hedenäs, 1997); however, they actually represent morphologically and genetically distinct species, although the latter proved to be a truly bipolar species that reached SE Australia along the Indomalayan and Melanesian track (Saługa et al., 2018). It is likely that forthcoming studies of the putative bipolar bryophyte species may reveal additional similar surprising discoveries.

The dramatic gaps in the geographical ranges of bipolar species are most often explained by long-distance dispersal via either wind currents or migrant birds (Lewis, Rozzi, & Goffinet, 2014), which serve as drivers for bipolar distribution between hemispheres. It can be either in one event, in the case of species exhibiting strict bipolarity, or a gradual process via trans-equatorial “mountain-hopping” or “stepping-stone” dispersal along the mountain tracks across the tropics, which is the most probable strategy in transitional bipolarity. The former dispersal event has been confirmed by some molecular phytogeographic studies on mosses (Lewis, Behling, et al., 2014; Piñeiro et al., 2012).

In contrast to more southerly sub-Antarctic and peri-Antarctic islands, which were glaciated to varying extents during the Last Glacial Maximum (Birkenmajer et al., 1985; Hodgson et al., 2014; Van der Putten, 2004, 2009, 2010), the islands of the Tristan da Cunha archipelago have never been glaciated; their climate has been relatively constant, at least during the last 43,000 years (Bennett et al., 1989). Therefore, they have been practically always available for colonization and their current flora is composed mostly of taxa that arrived via long-distance dispersal from conterminous land masses, including South America and Africa. Because the core of the bryophyte flora of these islands comprises cool-adapted South American temperate species, it is obvious that they arrived from this continent via long-distance dispersal, since the archipelago lies mid-way on their migration route to Africa.

Species with an amphi-Atlantic distribution pattern are well represented in the bryophyte flora of these neighboring continents. This group comprises about 80 species of liverwort (Ellis, Bakalin, et al., 2013; Gradstein, 2013) and over 80 species of moss (Bednarek-Ochyra et al., 1999; Ellis, et al., 2014; Ellis, Bednarek-Ochyra, et al., 2013; Frahm, 1982; Ochyra et al., 1992; Ochyra & Ireland, 2016; Ochyra, Wesche, et al., 2002). They are mostly represented by tropical lowland and montane species; however, this group also consists of a small group of south-cool-temperate and sub-Antarctic species (e.g., Bednarek-Ochyra, 2014b, 2018; Bednarek-Ochyra & Ochyra, 1998, 2010, 2012a; Blockeel et al., 2009, 2010; Ellis, Aleffi, et al., 2015; Ochyra, 1987, 2010; Ochyra & Bednarek-Ochyra, 2013; Ochyra & Bell, 1984; Ochyra & Lewis Smith, 1998; Ochyra & Lightowlers, 1988; Ochyra & Váňa, 1989). A significant number of these species is known to occur in the Tristan da Cunha archipelago. *Pseudotaxiphyllum elegans* apparently belongs to this group; it is very likely that its populations in this area are derived from the population from the Falkland Islands or still unknown populations from mainland South America. In fact, this species can be considered as a semi-Afro-American species since it does not extend to the African continent, but its range extends to only mid-way between South America and Africa. A similar distribution is also exhibited by *Dilutineuron laevigatum* (Bednarek-Ochyra, 2006), *Hygrodicranum falklandicum* (Blockeel et al., 2007), *Trichostomum aequatoriale* Dixon, and *Dicranella vaginata* (Hook.) Cardot (Dixon, 1960).

## Acknowledgments

The authors are very grateful to Dr. Robert R. Ireland, Ottawa, Canada, for his important suggestions and valuable comment on the status of *Isopterygium tristaniense*; Professor Rodney D. Seppelt, Bundall, Queensland, Australia, for his kind improvement of the English language and comments on the manuscript; and to the Curator of Bryophyta at FH for kindly allowing us to study the type material of this species.

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