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Ferns and Lycophytes as new challenges

Life history of an endemic and threatened species: *Pteris congesta*

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Abstract

Pteris congesta an endemic and endangered species was investigated to identify morphological differences between its sterile and fertile leaves. Our findings have unveiled, leaf dimorphism in both morphology and growth patterns between fertile and sterile leaves. The sterile leaves petioles exhibited equivalent growth to the laminae, achieving complete leaf expansion within a month. In contrast, the petioles of fertile leaves elongated more than twice the size of the leaf blades that remain closed for the initial 30 days. Spore germination was carried out in both sterile and non-sterile soils, and juvenile sporophytes were cultivated to allow for morphological comparisons with those collected from the wild. One month after sowing the spores germinated in both soils resulting in a uniseriate germ filament *Vittaria*-type, and differentiated into laminar gametophytes, forming a *Ceratopteris*-type prothallus. The first leaf of the sporophyte emerged two months after sowing, and its development was completed one month later. Based on our studies, we propose that seedlings cultivated from spores germinated in soil can be used for the reintroduction of endangered fern species.

Key words: Atlantic Forest, conservation, gametophyte, sporophyte development, spore germination.

Resumo

Pteris congesta, uma espécie endêmica e ameaçada de extinção, foi investigada para identificar diferenças morfológicas entre suas folhas estéreis e férteis. Revelamos que há dimorfismo foliar tanto morfológico como também nos padrões de crescimento entre as folhas férteis e estéreis. Os pecíolos das folhas estéreis crescem de forma equivalente às lâminas e alcançam a expansão foliar completa em um mês. Em contraste, as folhas férteis alongam mais que o dobro do tamanho das lâminas foliares e permanecem fechadas nos primeiros 30 dias. A germinação de esporos foi realizada em solos estéreis e não estéreis, e esporófitos juvenis foram cultivados para permitir comparações morfológicas com aqueles coletados na natureza. Um mês após a semeadura, os esporos germinaram em ambos os solos resultando em filamentos germinativos unisseriados do tipo *Vittaria* que se diferenciaram em gametófitos laminares, formando um prótalo do tipo *Ceratopteris*. A primeira folha do esporófito emergiu dois meses após a semeadura, e seu desenvolvimento foi concluído um mês depois. Com base em nossos estudos, propomos que mudas cultivadas a partir de esporos germinados no solo possam ser utilizadas para a reintrodução de espécies de samambaias ameaçadas de extinção.

Palavras-chave: Mata Atlântica, conservação, gametófito, desenvolvimento do esporófito, germinação de esporos.

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Introduction

Studies on the development of a population in its natural habitat allow researchers to recognize the sequential stages of the organism's life history, evaluate its growth, and gain a greater understanding of its dynamics, findings that are crucial to informing efforts to protect the species (Carvajal-Hernández *et al.* 2017; Sharpe & Mehltreter 2010). These observations provide morphological information on the species' juvenile stages, helping to identify in its habitat, and are also really important for conservation.

Pteris (Pteridaceae) is one of the largest genera of ferns (Zhang *et al.* 2015), has a pantropical distribution, and occurs in tropical, subtropical, and temperate climates with around 250 species worldwide (PPG I 2016; Zhang *et al*. 2015). There are 24 species of *Pteris* in Brazil, of which 17 occur in the Atlantic Forest (Prado & Hirai 2020). *Pteris congesta* J. Prado is one of the six *Pteris* species endemic to this country and has been categorized as endangered (EN) within the criteria established by the IUCN (Condack *et al.* 2018; Prado 1993; Prado *et al*. 2013; Prado & Hirai 2020). *Pteris* has morphological variety among its species regarding lamina architecture, venation pattern, and indument (Prado & Windisch 2000).

Pteris congesta has non-green spores as the majority of the ferns (Lloyd & Klekowski 1970). These spores have storage physiology similar to orthodox seeds, and most can remain viable for months or years, depending on the species, if kept under controlled laboratory conditions (Ballesteros 2010; Pedrero-López *et al.* 2021). On the other hand, the viability of propagules in their natural environment, such as in the soil bank under natural conditions, expresses their ecological longevity (Vázquez-Yanez & Orozco-Segovia 1993). Studies on the viability and vigor of spores in their natural habitat show that germination and gametophyte development is more successful when spores are buried deeper in the soil (Pedrero-López *et al.* 2021).

This study seeks to contribute to the understanding of the biology, and habitat of *P. congesta*. Our objectives are to (I) describe the development and morphological differences through the life stages of sterile and fertile leaves, and (II) evaluate the germination potential of spores in the soil with two treatments, using sterile and non-sterile soil, to produce juvenile sporophytes.

Material and Methods

The study was conducted in the municipality of Rio de Janeiro, Brazil, in an area located within the buffer zone of the Tijuca National Park, along the trail to Pedra do Marinheiro (22°58'17"S, 43°13'30"W). The location is adjacent to the Arboretum of the Botanical Garden Research Institute of Rio de Janeiro and was used to monitor the development of fertile and sterile adult and juvenile leaves. The leaves were observed, and recorded every month for each individual, from the emergence of the fiddlehead until senescence.

The distribution of the species was established by collections available on the Reflora - Herbário Virtual (<http://reflora.jbrj.gov.br/reflora/herbarioVirtual/>), Pteridoportal (2021), and SpeciesLink (<https://specieslink.net/>) platforms (Fig. 1). The specimen's description was based on herbarium material and population observations.

The germination potential of the spore was verified under two conditions using sterile and non-sterile soil. The topsoil samples, about 5 cm deep, were collected near individuals with the largest number of fertile leaves, and were placed in transparent plastic boxes in the laboratory. Additionally, fertile pinnae with mature sporangia were placed into paper bags and left to dry at room temperature to spore release, and these spores were sown in sterile three Petri dishes containing sterilized soil for four months. Both treatments were maintained in the laboratory under controlled conditions, and were packed in transparent plastic bags to avoid dehydration and contamination.

Juvenile sporophytes were transplanted to transparent plastic boxes containing sterilized soil, packed in transparent plastic bags like a micro-greenhouse moist. Young sporophytes of *Pteris congesta*, about 10 cm in height, were collected in the field for morphological comparison with those germinated in the laboratory.

Results and Discussion

All information about the development of fertile and sterile leaves, such as length, height, color, texture, and the presence of sporangia and spores was recorded during the monthly monitoring of the specimens from the Pedra do Marinheiro population**.** A distinct pattern was observed in the development of fertile and sterile leaves (Fig. 2a-j). This pattern consisted of differences in petiole length and laminar expansion over time, beginning with the emergence of the fiddlehead.

The petioles of the sterile leaves grew as much as the laminae, with a proportion of 1:1, with complete leaf expansion after 30 days. The petioles of the fertile leaves, however, elongated to more than twice the size of the leaf blades, which remained closed for the first 30 days (Fig. 2a-c). This same leaf growth pattern has been recorded in other taxa such as *Hemionitis arifolia* (Burm. F.) T. Moore (Pteridaceae: Dickason 1946) and in *Polybotrya* species (Dryopteridaceae: Moran 1987a), which have dimorphic leaves (Fig. 2c-f). Thus, there seems to be a dimorphic growth pattern between fertile and sterile leaves. In addition, the sterile leaves had a petiole only 1/3 the length of the petiole of the fertile leaves (Fig. 2e,h). When the blades of the fertile leaves expand, it appears that the pinnules already have the false indusia on the margin with the brown sporangia, while the blades of the sterile leaves remain membranaceus (Fig. 2g,j). Both leaves become chartaceous in adulthood. Our results showed, for the first time and in a detailed way, leaf dimorphism in *Pteris congesta* through the differences in the morphology and growth pattern between fertile and sterile leaves (Fig. 2d-e,h). The concept of leaf dimorphism in ferns can address the morphological differences between fertile and sterile leaves, leaf longevity, and physiological reactions (Dickason 1946; Lellinger 2002; Moran 1987b; Wagner & Wagner 1977).

Laminas with sporangia had a petiole up to twice as large as the leaves before the leaf expansion over a period of 30 days. Meanwhile, the petiole and blade of sterile leaves grew proportionally (1:1), with complete laminar expansion in the same period. Petiole elongation prior to lamina formation has also been observed in the development of *Adiantopsis radiata* (L.) Fée and *Pteris denticulata* Sw., species of the Pteridaceae, under natural conditions (Ranal 1991).

Two non-exclusive hypotheses can explain leaf dimorphism in ferns, especially in herbaceous species. In the first hypothesis, larger petioles allow fertile leaves to be farther from the ground, which can favor the dispersion of spores by wind and rain (Britton & Watkins 2016; Watkins *et al.* 2016). In the second hypothesis, the larger size of petioles promotes a change in the position and height of fertile leaves, favoring photosynthetic activity by reducing the shading caused by sterile leaves

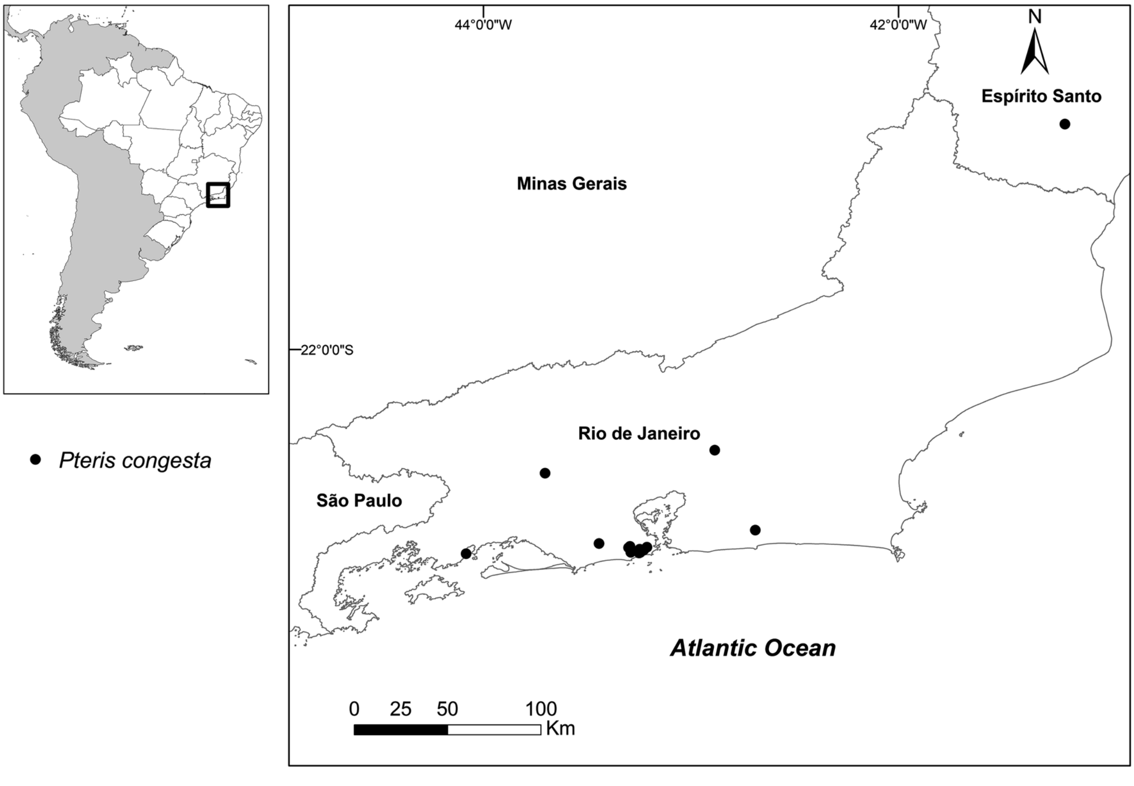

Figure 1 – Global distribution of *Pteris congesta* based on the specimens deposited in herbarium collections.

(Givnish 1988; Kikuzawa *et al*. 1996; Kikuzawa 2003; Watkins *et al.* 2016). Studies comparing the photosynthetic activity of fertile and sterile leaves and spore dispersal are necessary to test these hypotheses.

Pteris congesta is a terrestrial plant about 45 cm high with an erect to decumbent stem protected by scales, without trichomes. The morphological analysis revealed that there are different types of scales (Fig. 3a-c) across the sporophyte, as shown in Table 1 and Fig. 3. Petioles are subcylindrical, sulcate adaxially, green when alive, or light brown to yellowish-green when dry, glabrous, with scales or not. Rachises are sulcate adaxially and narrowly winged glabrous or with trichomes. Trichomes, when present, can be hyaline acicular along the

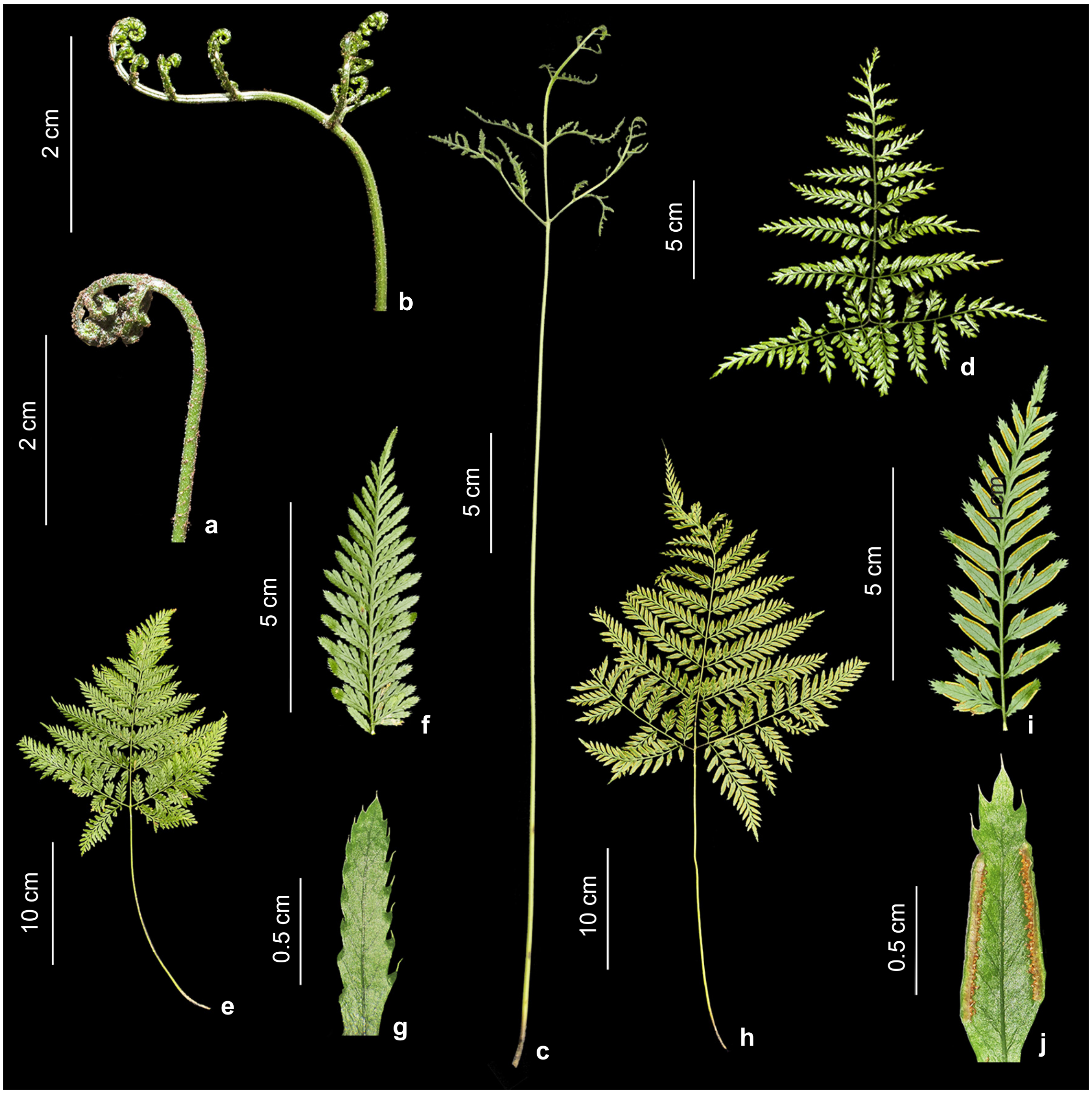

Figure 2 – a-j. Detail of the fertile and sterile leaves of *Pteris congesta* at different life stages showing the differential characters for species recognition, highlighting its life stages and morphology – a-b. detail of the apex of the fiddlehead; c. young fertile leaves in development with elongated petiole and unexpanded blade; d. young sterile leaf in development with expanded blade; e. sterile adult leaf; f. detail of sterile pinna; g. detail of the sterile pinnule with denticulate-ciliate margins; h. fertile adult leaf; i. detail of fertile pinna; j. detail of fertile pinnule with marginal sori. (Photos: Carlos D.M. Ferreira).

Table 1 – List of the morphological characters of the scales and their variations on the stem of *Pteris congesta*.

Scales	Only on the apex of the stem	Only along the stem	Occur on the apex and along the stem
Shape and size	Oblong-lanceolate (1.5 – 3.5 × 0.1 – 0.3 mm)	Linear (c. 2.5 × 0.2 mm)	Lanceolate (2 – 3.5 × c. 0.2 mm)
Base	cordate	truncate	cordate
Apex	acute	acute	acute
Margin	entire or denticulate (can present linear projections)	entire or denticulate	entire or with linear projections
Color	concolor, with light brown to black base	concolor, light brown	dichromatic, with translucent light brown base to dark reddish-brown to the apex

adaxial groove or sparse dark brown to red catenates on the abaxial surface usually located in the axils of the pinnae (Fig. 3d-e). Pinnae are opposite, chartaceous, denticulate-ciliate in the margins (Fig 2f,g) or entire in the portion of the sori when they are fertile (Fig. 2j). Venation is free, with veins simple or bifurcate, glabrous, about 10 pairs per pinnule. Sori are marginal, located in the median portion of the pinnules, protected by false linear, membranaceus, concolor, and light green indusia. Sporangia are brown, with about 32 spores per capsule. Spores are tetrahedral-globose, trilete (Fig. 3f).

The morphological description of *Pteris congesta* (Prado & Windisch 2000) is corroborated here, while the types of scales and trichomes of the sporophyte were detailed based on live specimens and the revision of more collections. This information on the species' morphology can help recognize sequential categories of life stages and contribute to studies of population dynamics (Sharpe & Mehltreter 2010).

Although little used in studies of tropical ferns (Ramírez-Trejo *et al.* 2004; Ranal 2003), spore germination trials can help indicate dispersal ability, spore viability under natural conditions, and the population regeneration of plant communities (De Groot *et al*. 2012; Ranal 2003; Tryon 1970). The soil collected at the site of occurrence of the species and incubated under controlled laboratory conditions to monitor the germination of spores showed potencial to development gametophytes and sporophytes of *Pteris congesta*.

Germination takes place on both soil treatments a month after sowing (Fig. 4a-g). The spore germination (Fig. 4a) is of the *Vittaria*-type (Fig. 4b), resulting in a uniseriate germ filament (Nayar & Kaur 1971). This filamentous gametophyte phase is brief and begins to differentiate into laminar gametophytes (Fig. 4c), which develops forming a *Ceratopteris*-type prothallus (Fig. 4e) (Nayar & Kaur 1971). Two months after sowing, adult bisexual and cordiform-gametophytes (Fig. 4d) developed on the soil surface. The gametangia appeared on the abaxial surface of the gametophyte with archegonia (ca. 7) near the notch and many antheridia (ca. 20) distributed mainly towards the base, mixed between rhizoids (Fig. 4f,g).

The first leaf of the sporophyte appeared 2 months after sowing and one month later the development of the leaf was complete. Due to variations in environmental conditions during cultivation this period can be variable (Ramírez-Trejo *et al.* 2013). The use of seedlings propagated from the soil spore bank can be an alternative for the reintroduction of fern populations, especially when *in vitro* propagation is not an effective technique (Commander *et al.* 2018; Lindsay & Dyer 1990). The sporophyte and the gametophyte have similar ecological requirements for their survival, however the gametophyte, due to its simpler morphology, is more susceptible to lack of moisture in the substrate and in the atmosphere (Nayar & Kaur 1971). Thus, controlled conditions in the laboratory may facilitate obtaining the greatest number of sporophytes from spore germination.

The present morphological study of the young phases of *P. congesta* has enabled identifying the fern in its natural habitat. Diagnostic characters were observed in sporophytes measuring 3 cm in height, such as: winged and adaxially sulcate rachis, hyaline trichomes, pinnules with denticulate-ciliate margin, triangular blade, and free veins, which reached 15 cm in height after 24 months. It was verified from those diagnostic characters that the young individuals collected in the field are the same as those germinated in the laboratory.

During the process of propagation from the soil spore bank, small quantities of seedlings from the genera *Adiantum*, *Macrothelypteris*, and *Nephrolepis* were also recognized. The germination of different species of ferns in the soil spore bank may indicate the ability of spore dispersal over large distances, mainly through the wind, and that their viability can be maintained under natural conditions (De Groot *et al.* 2012; Ranal 2003; Tryon 1970).

Material examined: RIO DE JANEIRO: Rio de Janeiro, 1850, *D. Howard* (NY00812766); Serra de Jacarepaguá, 1876, *A.F.M. Glaziou 5337* (US); IX.1887, *E.H. Ule 887* (US); Cachoeira dos Primatas, Parque Nacional da Tijuca, 5.XI.2019, *L. Bastos 30* (RB); Corcovado, 1891,

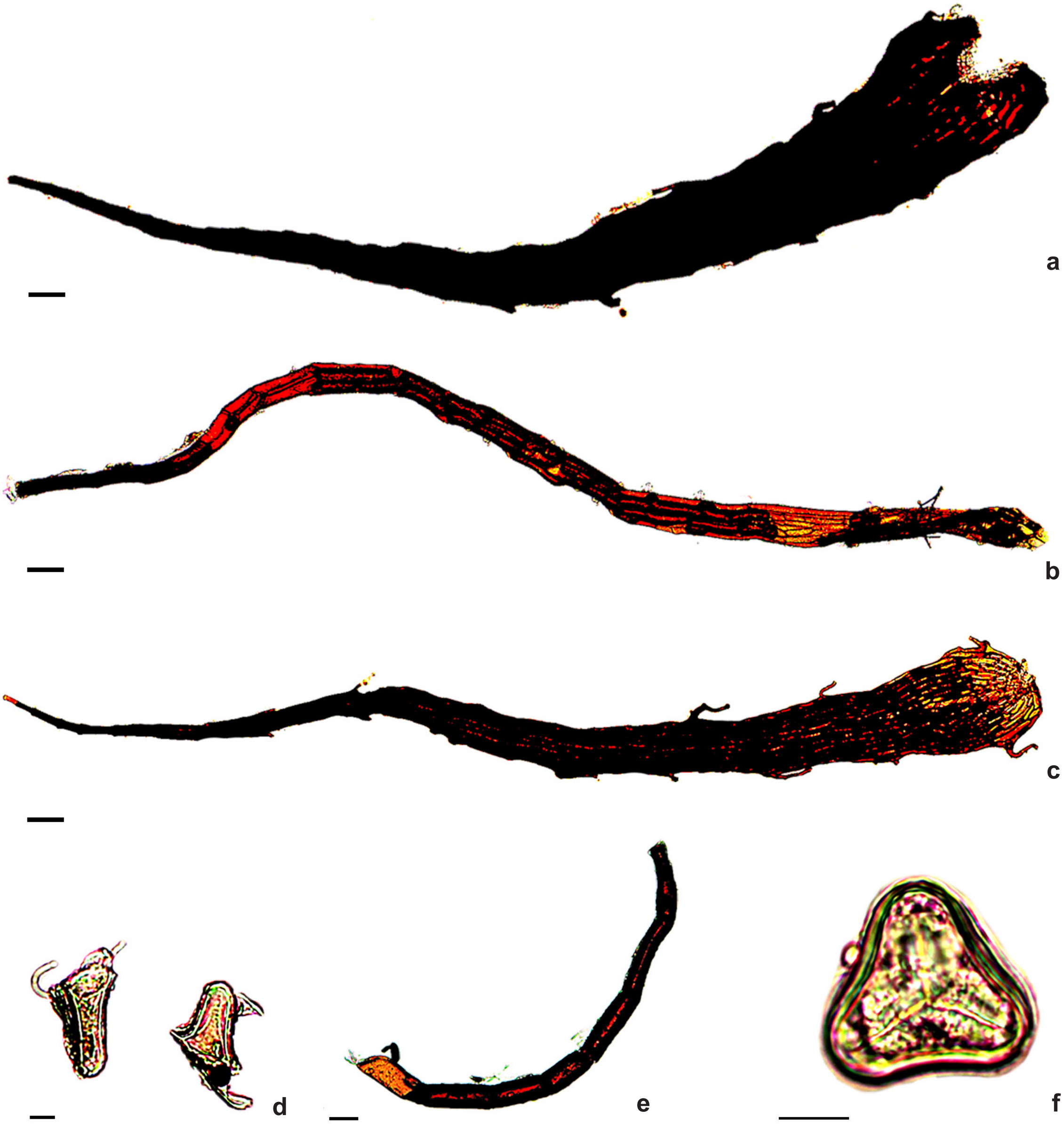

Figure 3 – a-f. Detail of the scales, trichomes and spores of *Pteris congesta* – a. scales of the stem apex; b. scales present along the stem; c. scales present at the apex and along the stem; d. detail of hyaline acicular trichomes along the adaxial groove; e. detail of trichomes dark brown to red catenates on the abaxial surface of the leaf; f. spore in polar view under light microscope. Scales: a, b, c. = 100 µm; d. = 10 µm; e. = 20 µm; f. = 10 µm.

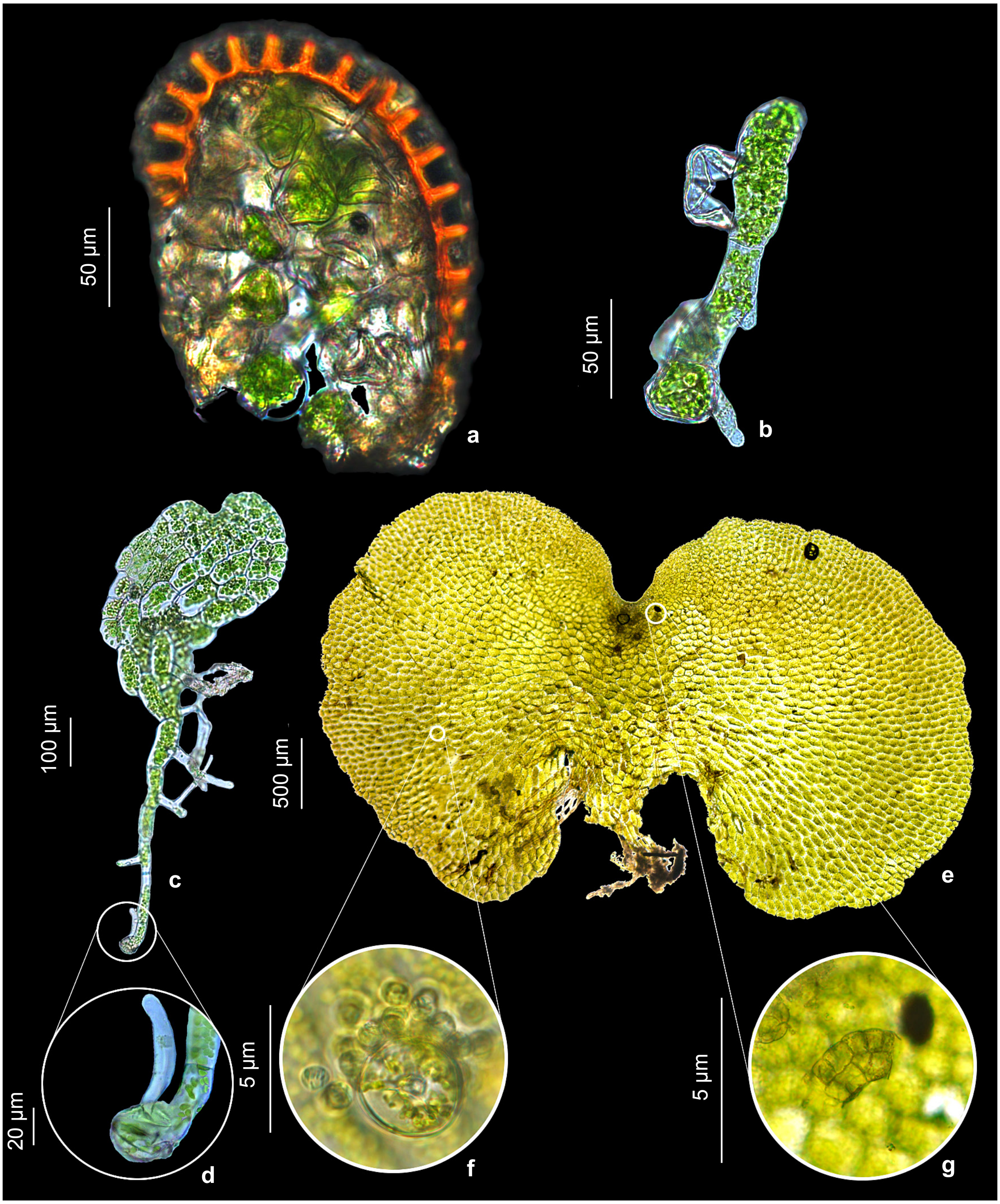

Figure 4 – a-g. Spore germination and gametophyte development – a. spore germination into sporangium; b. spore germination showing *Vittaria*-type gametophyte; c. differentiation of filamentous gametophyte phase into laminar gametophyte; d. detail of gametophyte with spore; e. developed gametophyte forming a *Ceratopteris*-type; f. detail of antheridia with antherozoids; g. detail of archegonia.

R. Rathbun (US01479199); 31.VIII.1911, *C. Osten 5534* (UC, US); 8.VII.1915, *J.N. Rose & P.G. Russel 20173* (NY, US); 1925, *C. Spannagel 384* (NY); Corcovado, *Saldanha* (RB36552); Gávea, mata das obras públicas, 8.V.1923, *L. Gurgel 48* (RB); Pedra Dois Irmãos, 26.XI.1928, *L.B. Smith 1353* (NY, US); Jardim Botânico, 30.VIII.1933, *P. Occhioni* (RB31641); matas do Pai Ricardo, 23.III.1945, *P. Occhioni 26* (RB); Sacopam, 6.VIII.1946, *A.P. Duarte 186* (RB); Mata do Rimo, reserva florestal do Jardim Botânico, 18.I.1969, *D. Sucre & P.I.S. Braga 4452* (RB); Pedra da Gávea, 10.XI.1974, *P. Carauta & L. Freire de Carvalho 1757* (PACA, RB); matas do Jardim Botânico, 24.V.1979, *M. dos Santos et al. 40* (RB); Pedra do Marinheiro, 4.VIII.1993, *C.M. Mynssen et al. 35* (ESA, RB); 9.IX.2014, *C.M. Mynssen et al. 1440* (NY, P, RB); Parque Estadual da Pedra Branca, 10.III.1994, *J.M.A. Braga et al. 1110* (RB); Pedra do Marinheiro, 8.IV.1999, *R. Marquete et al. 2977* (RB); Pico do Papagaio, Parque Nacional da Tijuca, 12.III.2008, *C.M. Mynssen et al. 1089* (RB); 4.X.2012, *C.M. Mynssen & B.K. Canestraro 1366* (RB). Mangaratiba, Reserva Rio das Pedras, 6.I.2000, *C.M. Mynssen, 297* (RB). Maricá, Cachoeira do Espraiado, 10.VI.2004, *S.L.S. Winter 138* (RB). Guapimirim, Estação Ecológica Estadual do Paraíso, 2.XII.2008, *C.E.S. Jascone 1236* (RB). Paracambi, Parque Natural Municipal do Curió, 1.V.2019, *G.B. Guarnier & I.A.A. Silva 17* (R). ESPÍRITO SANTO: Atílio Vivácqua, Moitão, Pedra do Coração, 25.IV.2007, *L. Kollmann 9662* (BHCH, MBML).

Our survey of herbarium specimens found a total of 30 specimens of *Pteris congesta* in herbarium collections. Most specimens come from the municipalities of Rio de Janeiro, Guapimirim, Mangaratiba, Maricá, and Paracambi, collected at 100–800 m of altitude. In the Espírito Santo state, one occurrence has been recorded, in the municipality Atílio Vivácqua (Pedra do Coração), from which a sample was collected at an altitude of 700 m.

The population from Pedra do Marinheiro grows on steep slopes, close to rocky outcrops in partially shaded places that are less impacted by human trampling, or in groups of a few isolated individuals on the edge of trails. Studies on the habitat importance and dispersal ability of rare fern species have shown that, on a regional scale, dispersal limitation plays an important role in ferns (Tájek *et al.* 2011). An investigation of the environmental characteristics of the locations where *Pteris congesta* occurs could point to factors related to the limitation of its distribution.

Since *Pteris congesta* is an endemic and endangered species that may be affected by habitat alteration and loss (Condack *et al.* 2018; Fernandes *et al.* 2004), the use of plants propagated from the spore bank of the soil can be an effective strategy for the conservation of this species, as this method contributes to a reservoir of high genetic diversity in ferns (Hock *et al.* 2006; Schneller 1998).

Our studies reveal that there is leaf dimorphism both morphologically and also in growth patterns between fertile and sterile leaves of *Pteris congesta*. Specifically, the petioles of sterile leaves demonstrate growth equivalent to the blades, resulting in complete leaf expansion within one month. In contrast, the petioles of fertile leaves elongate to more than twice the length of leaf blades that remain closed for the first 30 days.

Germination occurred in both soil treatments after one month resulting in a uniseriate germ filament *Vittaria*-type, and differentiated into laminar gametophytes, forming a Ceratopteris-type prothallus.

Based on our findings, we suggest that spore-cultivated seedlings can be effectively employed for the reintroduction efforts aimed at conserving the endangered fern species.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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