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Oncophoraceae (Bryophyta): a palynological treatment of species occurring in the Americas

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Abstract: Oncophoraceae are acrocarpous mosses that predominantly grow as tufts or cushions and especially occur on rocks and soil. The recognition of Oncophoraceae as a distinct family, as well as its generic circumscription, is not consensus among authors, and the pursuit for new information to improve its characterization is incessant. The present work aims to characterize the spore morphology and ultrastructure of 19 species (eight genera) occurring in the Americas and to evaluate the relevance of palynological data to circumscribe species, contributing to support other palynological studies. Observations were performed under Light and Electron (Scanning and Transmission) Microscopes. A Cluster Analysis was performed in order to evaluate the meaning of the palynological data, especially concerning the establishment of the species circumscription. Spores are monads, small to medium sized (10.40 to 44.20 µm), radially symmetric, subcircular in amb, heteropolar or apolar; the surface is ornamented by granules, gemmae and bacula. Anisomorphic spores were observed in eight studied species and are reported herein for the first time. The Cluster Analysis shows two groups with low similarity, which primarily differ by the polarity of the spores. The circumscription of *Kiaeria* and *Cynodontium* is corroborated by palynological characterization and endorsed by Cluster Analysis.

Key words: Bryophytes, cluster analysis, morphology, mosses, Palynology, spores.

INTRODUCTION

Oncophoraceae M. Stech are acrocarpous mosses, small to medium sized, growing in tufts or cushions, rarely pendant, on rocks or soil, and less frequently on trees. The stems are short, simple or sparingly branched; the leaves are lanceolate to narrow-lanceolate and oblong at the base. The capsules are immersed to exserted, ovoid to pyriform; the peristome is simple, having 16 teeth (Frahm 2002, Frey & Stech 2009, Goffinet et al. 2008, Gradstein et al. 2001, Stech & Frey 2008).

The family includes about 100 species of wide distribution and high morphological variation, grouped in 13 genera: *Arctoa* Bruch & Schimp., *Cynodontium* Bruch & Schimp., *Dicranoweisia* Lindb. ex Milde, *Glyphomitrium* Brid., *Holodontium* (Mitt.) Broth., *Hymenoloma* Dusén, *Kiaeria* I. Hagen, *Oncophorus* (Brid.) Brid., *Oreas* Brid., *Oreoweisia* (Bruch & Schimp.) De Not., *Pseudohyophila* Hilp., *Rhabdoweisia* Bruch & Schimp., and *Symblepharis* Mont. (Frey & Stech 2009).

Since the 19th and 20th centuries, these genera were mostly treated in Dicranaceae (Schimper 1856) or Rhabdoweisiaceae (Limpricht 1904) in different circumscriptions, including variations in levels of subfamilies or tribes (Brotherus 1924, Crosby et al. 1999, Fleischer 1900, Vitt 1984).

Stech (1999a, b) highlighted the need for taxonomic revision of the group, which was sought by La Farge et al. (2002), Ochyra et al. (2003), Tsubota et al. (2003), Hedderson et al.

(2004), Stech & Frey (2008) and Zander (2008). But the relationship between these species has not yet been completely resolved (Cox et al. 2010, Stech et al. 2012). Increasing the number of morphological information of Oncophoraceae species is very important to support the taxonomy, especially considering palynological data, which are still scarce for the group.

Most works that provide information on spores of Oncophoraceae species are taxonomic works that only include size and colour indication for some species (Crundwell 1960, Eckel 2017, Hedderson & Blockeel 2006, Hedenäs 2017, Newmaster 2017, Ochyra & Bednarek-Ochyra 2013, Rhotero 2009, Robinson & Bowers 1974, Tan & Schofield 1980, van Rooy 1991, 1992, Weber 2017). In studying spores of Dicranaceae, Luizi-Ponzo & Barth (1999) described spores of *Oreoweisia brasiliensis* Hampe as small and granulate; currently, this species is included in Oncophoraceae (Frey & Stech 2009).

The relevance of palynological knowledge to the taxonomy has already been demonstrated for different plant groups (Silva et al. 2016, Gorrer et al. 2020, Pacini & Franchi 2020); dealing with bryophytes, some authors have also evidenced this importance (Brown et al. 2015, Caldeira et al. 2006, 2009, 2013, Estébanez et al. 1997, Luizi-Ponzo & Barth 1998, 1999, Luizi-Ponzo & Melhem 2006a, b, Luizi-Ponzo & Silva-e-Costa 2019, Medina & Estébanez 2014, Rocha et al. 2008, Savaroğlu 2015, Savaroğlu & Erkara 2008, Savaroğlu et al. 2007, 2017, Silva-e-Costa et al. 2017, Silva-e-Costa & Luizi-Ponzo 2019, Yano & Luizi-Ponzo 2006, 2011). Passarella & Luizi-Ponzo (2019) studied spores of Amphidiaceae, a monogeneric family that has a historical relationship with Oncophoraceae species (La Farge et al. 2002, Stech 1999b).

For mosses, spores are characterized by being generally unicellular, with sporoderm formed by at least three layers: intine, exine and perine, whose chemical constitutions have already been indicated as distinct (McClymont & Larson 1964, Mogensen 1981, 1983, Neidhart 1979, Olesen & Mogensen 1978). The ornamentation is often only formed by the perine, which contains sporopolenin (Brown & Lemmon 1980, 1981, 1984, 1988, Mueller 1974, Neidhart 1979, Olesen & Mogensen 1978), allowing these spores to occur in current and past sediments.

The palynological study proposed herein aims to describe the spore morphology and ultrastructure of 19 Oncophoraceae species occurring in the Americas, aiming to broaden the morphological data employed for their characterization, as well as to provide information to support palynological studies from different occurrences.

MATERIALS AND METHODS

We employed herbarium material from the following collections to perform this study: the Canadian Museum of Nature Herbarium (CANM), the Maria Eneyda P. Kauffmann Fidalgo Herbarium (SP), the Universidade de Brasília Herbarium (UB), and the Museu Nacional do Rio de Janeiro Herbarium (R). The acronyms are in accordance to Thiers (2020).

We studied species that occur in the Americas, but some of them are also present in other continents. In order to examine as many specimens as possible, all available exsiccates that presented mature capsules were examined, even if they were from another continent. The available material which had mature capsules were selected, totalling 19 species, namely: *Arctoa fulvella* (Dicks.) Bruch & Schimp.- United States of America: Washington, Pierce. W. B. Schofield 22265 (CANM); Canada: Queen Charlotte Islands. W.B. Schofield & J. Spence 84092 (CANM); New Zealand: Bay of Islands, R. J. Belland 4345

(CANM); *A. hyperborea* (Gunnerus ex With.) Bruch & Schimp. - Greenland: Tasilac, K. Holmen s/n (CANM 227256); *Cynodontium gracilescens* (F. Weber & D. Mohr) Schimp. - Austria: Tirel. A. de Degen s/n (R103455); *C. polycarpon* (Hedw.) Schimp. - Germany: Gotha, Waldmurchen. Trogel s/n 1887 (R80457); Germany: Gotha, Turingia., Dietharz s/n (R80452); *C. strumiferum* (Hedw.) Lindb. - Canada: Ontario, Thunder Bay, P. Barclay 10736 (CANM); Germany: Gotha, Inselsberg (R80454); *C. strumulosum* Müll.Hal. & Kindb. - Canada: Manitoba, Gillan, H.A Crum & W.B. Schofield 7499 (CANM); *C. tenellum* (Schimp.) Limpr. - Canada: Ontario, Kenora, W.B. Schofield 27183 (CANM); Canada: Ontario, Kenora, R.F Cain s/n (SP 171291); *Dicranoweisia cirrata* (Hedw.) Lindb. *ex* Milde - Canada, Lake County (SP 458819); Finland, Aland, Hammarland, Hamnskär, Sanna Huttunen s/n (SP 458687); United States of America: California, San Mateo, J. R. Shevock & K. Kellman 41829 (UB); United States of America: Colorado, Middle Boulder Creek, R.R. Ireland 16760 (CANM); *D. crispula* (Hedw.) Milde - Canada: Quebec, Iles des Foreus, R. R. Ireland 20871 (CANM); Canada: Quebec, Laval University, R. R. Ireland 20886 (CANM); Belgium: Ardenas, Ambleve, J.-P. Frahm s/n (SP 147043); Canada: Quebec, Lac Guillaume-Delisle, R. R. Ireland 21125 (CANM); *Kiaeria falcata* (Hedw.) I. Hagen - United States of America: Washington, Austin Pass, W.B. Schofield 74282 (CANM); Canada: Vancouver, Arrowsmith, F.M. Boas 1523 (CANM); Canada: Vancouver, Cypress Bowl, W.B. Schofield 74202 (CANM); *K. glacialis* (Berggr.) I. Hagen - Canada: Nain, Torngat Mountains National Park, T. Hedderson 5168 (CANM); Canada: Nain, Torngat Mountains National Park,T. Hedderson 5106 (CANM); Canada: Quebec, Ungava Bay, D. Weber 1386 (CANM); *K. starkei* (F. Weber & D. Mohr) I. Hagen - Canada: Alberta, H. Crum & W. B. Schofield 5983 (CANM); Canada: Cassiar, Omineca Mts., Peak Range, Mt. Hartley, R.R. Ireland & G. Bellolio-Trucco 18698 (CANM); Canada: Alberta, Boggy, Waterton Lakes National Park, H. Crum & W. B. Schofield 6097 (CANM); Canada: British Columbia, Moresby Island, W.B. Schofield 25093 (CANM); *Oncophorus virens* (Hedw.) Brid. - Canada: Newfoundland-Labrador: Halmilton Falls, P. Kallio s/n (CANM 118578); *O. wahlenbergii* Brid. - United States of America: Shelton, Kennedy Natural Preservation Area, J. Doubt DRBB28 (CANM); Canada: Ontario, Hastings, R.R. Ireland 16252 (CANM); England: Gloucester, R.R. Ireland, A.W. Dugal & L. M Ley 23826 (CANM); *Oreas martiana* (Hoppe & Hornsch.) Brid. - Germany: Staiermark, Terrach, Kiluprein, J. Breidler s/n (R80449); *Oreoweisia brasiliensis* Hampe - Brazil: Rio de Janeiro, Parque Nacional do Itatiaia, A. Schäfer-Verwimp & Verwimp s/n (SP 398451); Bolivia: La Paz, Laguna Huichicani, M. Lewis 87446 (SP); Brazil: Espírito Santo, Iúna, Parque Nacional do Caparaó, D. M. Vital & W. R. Buck 11799 (SP); *O. laxiretis* Broth. ex Herzog - Russia: Duitama, R.R. Ireland 23648 (CANM); *Rhabdoweisia crispata* (Dicks. *ex* With.) Lindb. - Canada: Ontario, Haliburton Co., Boshkung Lake, R.F. Cain & H. Williams s/n (SP 171370); and *R. fugax* (Hedw.) Bruch & Schimp.- Hungary, Comitat Beszteroze-Naszed, Dr. Degen s/n (R 103485); Poland, Carpathians,Tatra Mountains, R. Ochyra s/n (CANM 171428); Luxembourg: Berdorf, Valley of the Aesborach (SP 230857).

The spores were observed under Light Microscopy (LM), and Scanning Electron Microscopy (SEM). Transmission Electron Microscopy (TEM) was employed to confirm sporoderm strata definition.

For LM observation, the spores were prepared and analysed by the methods of Wodehouse (1935) and acetolysis of Erdtman (1960), following the adjustment proposed by Luizi-Ponzo & Melhem (2006b) for bryophytes. For SEM analysis, the capsules were fixed in glutaraldehyde and post-fixed in osmium

tetroxide; dehydrated in a graded ethanol series, and then dried out in a Critical Point dryer. Spores were subsequently dispersed upon stubs with double-sided carbon tape, and covered with a 20nm gold layer to be observed.

For observations under TEM, the capsules were fixed in glutaraldehyde and post-fixed in osmium tetroxide, washed in buffer solution and dehydrated in a graded ethanol series. They were encased in Spurr resin (Spurr 1969) and heated to 70°C for 48h; the resin blocks were then sectioned and mounted on TEM copper mesh. The material was contrasted with uranyl acetate and lead citrate (Reynolds 1963) and then observed.

The largest diameter measures were obtained using a micrometric ocular coupled to a Light Microscope. One sample material was indicated as the standard for each species (indicated by * on Tables), and the other sample materials as comparison. For all isosporic taxa, three slides were prepared and 50 spores were taken at random for larger diameter measurements. For all anisosporous species, the largest diameter of 100 spores was measured randomly for both standard and comparison material. For heteropolar spores, in order to take polar (P) and equatorial (E) diameter measurements, 30 spores were observed in equatorial view.

Arithmetic mean (X), standard deviation (S), standard error (Sx), coefficient of variability (CV%), and 95% confidence interval (CI) are presented, as well as the minimum and maximum spore size (Xmin-Xmax) of each analysed material.

The data referring to the larger diameter, polar and equatorial diameter values did not meet the normality assumptions, and were therefore statistically analysed using the Kruskal Wallis test. Next, a posteriori Dunnett test was applied to identify the different treatments. The statistical analysis was developed in Past. 2.17c (Hammer et al. 2001).

By virtue of the slight thickness of perine and exine, these two layers were measured together, configuring the sclerine (Luizi-Ponzo & Barth 1998, 1999). Sclerine and intine were measured from 10 random spores, prepared according to the Wodehouse (1935) method (and observing the adjustment by Luizi-Ponzo & Melhem 2006b), and arithmetic means were obtained.

Spore description followed Punt et al. (2007) for the terminology, and spore size classes followed Erdtman (1952).

Line graphs are presented to evaluate the spore size distribution, in which the values of the larger spore diameters were included in frequency classes. For anisosporous species, spores within the range of the first peak class of the line graph were referred to as “smallest spores”, and spores within the range of the second peak are called “largest spores” (Rodrigues & Luizi-Ponzo 2015).

A binary matrix was elaborated to perform the Cluster Analysis with the palynological data of the analysed species, namely, spore size, polarity, presence of anisospory, sporoderm thickness, type of ornamentation and aperture area. The data were submitted to Cluster Analysis on Past ver. 2.17c software (Hammer et al. 2001), and using the Jaccard similarity index to verify the degree of similarity between the species.

RESULTS

The studied taxa have small to medium sized spores (Tables I, II), isomorphic or anisomorphic, in monads, with radial symmetry, subcircular amb, heteropolar or apolar (Tables III, IV); apertural region differentiated or not, subcircular, and may present distinct ornamentation from

Table I. Morphometric data of anisomorphic spores (measurements in micrometers, * standard material, the other, comparison ones).

Species names and sample information	Smallest spores					Largest spores				
	Xmin-Xmax	X ± Sx	S	CV%	IC 95%	Xmin-Xmax	X ± Sx	S	CV%	IC 95%
Arctoa hyperborea Holmen, s/n*(CANM 227256)	18.20-20.80	20.57 ± 0.17	0.68	3.31	20.39-20.74	22.10-36.40	27.58 ± 0.39	3.56	12.91	26.60-28.53
Cynodontium gracilescens Degen, s/n* (R 103476)	18.20-29.90	22.47 ± 0.31	3.06	16.02	21.60-23.33	31.20-35.10	31.85 ± 0.65	1.59	4.99	31.44-32.25
Cynodontium polycarpon Trogel, s/n* (R 80457)	18.20-27.30	22.18 ± 0.27	2.20	9.92	21.55-22.80	33.80-44.20	38.53 ± 0.55	2.78	7.22	37.81-39.24
Cynodontium polycarpon Dietharz, s/n (R 80452)	15.60-23.40	19.09 ± 0.17	1.60	8.38	18.63-19.54	28.60-41.60	33.00 ± 0.84	3.59	10.88	31.97-34.02
Cynodontium strumiferum Barclay, 10736* (CANM)	13.00-18.20	16.30 ± 0.25	1.82	11.17	15.82-16.76	19.50-33.80	23.92 ± 0.33	2.77	11.58	23.18-24.61
Cynodontium strumiferum s/d (R80454)	15.60-18.20	17.80 ± 0.14	0.92	5.17	17.53-18.06	19.60-36.40	24.19 ± 0.59	4.46	18.44	22.92-25.45
Cynodontium strumulosum Crum & Schofield, 749* (CANM)	20.80-28.60	22.78 ± 0.24	1.84	8.08	22.30-23.25	33.80-44.20	37.91 ± 0.44	2.88	7.60	37.16-38.65
Cynodontium tenellum Schofield, 27183* (CANM)	15.60-23.40	21.31 ± 0.32	1.89	8.87	20.81-21.87	24.70-41.60	31.80± 0. 55	4.58	14.40	30.62-32.97
Cynodontium tenellum Cain, s/n (SP 171291)	18.20-23.40	20.26 ± 0.18	1.55	7.65	19.18-20.70	26.00-39.00	32.64 ± 0.69	3.63	11.09	31.60-33.67
Oncophorus virens Kallio, s/n* (CANM 118578)	16.90-22.10	20.52 ± 0.20	1.31	6.38	20.17-20.86	22.10-31.20	34.99 ± 0.30	2.27	9.08	24.38-25.59
Oncophorus wahlenbergii Doubt, DRBB28 * (CANM)	10.40-18.20	15.36 ± 0.23	2.00	13.02	14.86-15.89	19.60-26.00	20.55 ± 0.12	0.63	3.07	20.38-20.71
Oncophorus wahlenbergii Ireland, 16252 (CANM)	16.90-18.20	18.09 ± 0.10	0.37	2.05	17.45-18.75	18.20-28.60	21.93 ± 0.19	1.80	8.20	21.41-22.40
Oncophorus wahlenbergii Ireland, 23826 (CANM)	13.00-18.20	16.35 ± 0.15	1.47	8.99	15.93-16.76	19.50-20.80	20.57 ± 0.12	0.51	2.48	19.86-21.27

Xmin-Xmax: minimum and maximum values of spores size diameter, X ± Sx: mean and standard error, S: standard deviation, CV%: coefficient of variation, IC 95%: confidence interval.

the rest of the surface. Sporoderm is formed by intine, exine and perine, measuring between 1.16 µm and 2.93 µm (Tables V, VI).

It was necessary to observe the spores under SEM for detailed description of the ornamentation due to the small size of the spores and discreet ornamentation processes.

The sporoderm surface is ornamented by gemmae, granula or bacula (Figs. 1a-p, 2a-o, 3a-o). The gemmae can be numerous, varying in size and overlapping (*Oreoweisia laxiretis*, Figs. 1k, 2a, 2b) or in small number and uniform size (*Oreas martiana*, Figs. 1l, 2c).

Granula are responsible for sporoderm ornamentation in most species. The granules may have different sizes, be individual or united, and may be united in the aperture region, forming globular processes (*Arctoa hyperborea*, Figs. 1c, 2f, 2g, 2h) or are associated to gemma (*Arctoa fulvella*, Figs. 1a, 1b, 2c, 2d). The exine may have small exposed areas (*Kiaeria starkei*, Figs. 1j, 2l) or be totally covered by ornamentation processes (*Oreoweisia brasiliensis*, Fig. 2m and *Kiaeria falcata*, Figs. 1i, 2i).

The bacula can be single or grouped and have uniform (*Rhabdoweisia fugax*, Figs. 3n, 3o) or variable distribution (*Rhabdoweisia crispata*, Fig. 3a). In the apertural area, they may be associated with single (*Rhabdoweisia fugax*, Figs. 3n, 3o) or grouped granula (*Dicranoweisia cirrata*, Figs. 1h, 3j-3m) and gemma (*Cynodontium*, Figs. 1e-1g, 3a-3h). The bacula in *Cynodontium tenellum*, Figs. 1g, 3g, 3h) are of different sizes and may be fused, associated to rugulate perine, while pila occur in *Cynodontium strumiferum*, Figs. 1e, 3e, 3f), in addition to bacula of different sizes.

A Cluster Analysis (Fig. 4) using the palynological characteristics (Table VII) shows a cophenetic index of 0.9634, demonstrating that the characteristics used for analysis are consistent, although the variation in spore size is large (Fig. 5). It was possible to group the 19 studied species into two large groups (Group A and Group B), and then into six subgroups (B1 to B6).

Group A: formed by the *Kiaeria* species: *K. falcata*, *K. glacialis*, and *K. starkei*, species which present apolar spores.

The spores are small in size (Table II) with unimodal distribution (Fig. 6a-c). The sporoderm surface is ornamented with granula, which may be grouped or overlapped, with different sizes and distributions. The exine is fully covered by the perine or it has small exposed areas (Figs. 1i, 1j, 2i-2l).

Group B: formed by the other studied species, all of them have heteropolar spores. This group was divided into six subgroups.

Subgroup B1: formed exclusively by the *Oreoweisia laxiretis*, species which has spores without a defined apertural area. The spores are small in size (Table II) with unimodal size distribution frequency (Fig. 6d) and the sporoderm surface is heavily ornamented with gemma, which can be uniform or varied in size and exhibit overlap (Figs. 1k, 2a, 2b).

Subgroup B2: formed by *Cynodontium gracilescens*, *C. polycarpon*, *C. strumiferum*, *C. strumulosum*, and *C. tenellum*, which present anisomorphic spores and sporoderm surface with different kinds of granula processes. The spores are small to medium in size (Table I), with bimodal spore size distribution (Fig. 6e-i). The sporoderm surface is ornamented with bacula, which may be single or united, gemma and granula. An apertural subcircular area is present, having a distinct ornamentation from the remaining surface of the sporoderm (Figs. 1e-1g, 3a-3h).

Subgroup B3: includes *Dicranoweisia cirrata*, *D. crispula*, *Oreas martiana*, and *Rhabdoweisia crispata* which exhibit isomorphic spores and sporodem with ornamentation processes other

Table II. Morphometric data of isomorphic spores (measurements in micrometers, * standard material, the other, comparison ones).

Species names and sample information	Xmin-Xmax	X ± Sx	S	CV%	IC 95%
Arctoa fulvella Schofield, 22265* (CANM)	15.60-28.60	20.65 ± 0.21	2.16	10.46	20.07-21.22
Arctoa fulvella Schofield & Spence, 84092 (CANM)	15.60-28.60	20.56 ± 0.21	2.17	10.55	19.94-21.17
Arctoa fulvella Belland 4345 (CANM)	15.60-23.40	18.59 ± 0.19	3.67	19.74	17.54-19.63
Dicranoweia crispula Ireland, 20871* (CANM)	13.00-18.20	14.27 ± 0.19	1.35	9.46	13. 88-14.65
Dicranoweia crispula Ireland, 20886 (CANM)	10.40-15.60	13.17 ± 0.23	1.26	9.57	12.18-14.52
Dicranoweia crispula Frahm, s/n (SP 147043)	13.00-16.25	14.19 ± 0.21	1.19	9.76	13.85-14.52
Dicranoweia crispula Ireland, 21125 CANM)	13.00-16.90	14.77 ± 0.21	1.15	7.79	14.44-15.09
Dicranoweisia cirrata s/d* (SP 458819)	13.00-20.80	17.34 ± 0.22	1.62	9.34	16.87-17.80
Dicranoweisia cirrata Huttunen, s/n (SP 458687)	15.60-22.10	17.98 ± 0.32	1.79	9.96	17.47-18.48
Dicranoweisia cirrata Shevock & Kellman, 41829 (CANM)	15.60-23.40	18.82 ± 0.29	1.59	8.45	18.36-19.27
Dicranoweisia cirrata Ireland, 16760 (CANM)	13.00-18.20	15.16 ± 0.31	1.75	11.54	14.62-15.65
Kiaeria falcata Schofield, 74282* (CANM)	13.00-20.80	16.77 ± 0.29	2.07	12.34	16.18-17.35
Kiaeria falcata Boas, 1523 (CANM)	13.00-18.20	15.47 ± 0.20	1.15	7.43	15.14-15.79
Kiaeria falcata Schofield, 74202 (CANM)	11.70-15.60	13.65 ± 0.19	1.06	7.77	13.34-13.95
Kiaeria glacialis Hedderson, 5168* (CANM)	18.20-26.00	21.24 ± 0.29	2.10	9.89	20.64-21.83
Kiaeria glacialis Hedderson, 5106 (CANM)	18.20-22.10	19.54 ± 0.23	1.29	6.60	19.17-19.90
Kiaeria glacialis Weber, 1386 (CANM)	15.60-23.40	19.93 ± 0.35	1.94	9.73	19.37-20.48
Kiaeria starkei Crum & Schofield, 5983* (CANM)	13.00-19.50	15.86 ± 0.21	1.49	9.39	15.43-16.28
Kiaeria starkei Ireland & Bellolio-Trucco, 18698 (CANM)	13.00-15.60	14.86 ± 0.18	1.00	6.73	14.57-15.14
Kiaeria starkei Crum & Schofield, 6097 (CANM)	13.00-16.90	15.21 ± 019	1.08	7.10	14.90-15.51

Table II. Continuation

Kiaeria starkei Schofield, 25093 (CANM)	13.00-18.20	15.25 ± 0.22	1.22	8.00	14.90-15.59
Oreas martiana Breidler, s/n* (SP 80316)	19.50-31.20	23.89 ± 0.32	2.30	9.63	23.23-24.54
Oreoweisia brasiliensis Schäfer-Verwimp & Verwimp, s/n* (SP 398451)	18.20-28.60	24.20 ± 0.38	2.70	11.16	23.43-24.96
Oreoweisia brasiliensis Lewis, 87446 (SP)	15.60-23.40	18.74 ± 0.32	1.76	9.39	18.23-19.24
Oreoweisia brasiliensis Vital, 901 (SP)	20.15-27.30	22.53 ± 0.37	2.02	8.97	21.95-23.10
Oreoweisia laxiretis Ireland, 23648* (CANM)	15.60-23.40	20.04 ± 0.19	1.39	6.94	19.64-20.43
Rhabdoweisia crispata Cain & Williams, s/n* (SP 171370)	15.60-23.40	18.63 ± 0.38	2.13	11.43	18.02-19.23
Rhabdoweisia fugax Degen, s/n* (R 103485)	13.00- 8.20	15.96 ± 0.16	1.14	7.14	15.63-16.28
Rhabdoweisia fugax Ochyra, s/n° (SP 171428)	15.60-20.35	18.82 ± 0.46	2.54	13.50	18.09-19.54
Rhabdoweisia fugax s/d (R 230857)	15.60-24.05	19.37 ± 0.38	2.12	10.94	18.76-19.97

Xmin-Xmax: minimum and maximum values of spores size diameter, X ± Sx: mean and standard error, S: standard deviation, CV%: coefficient of variation, IC 95%: confidence interval.

than granules. The spores are small in size (Table II) with unimodal spore size distribution (Fig. 6j-m), ornamented by bacula which may be single or grouped, and gemma (Figs. 1c, 1h ,1l, 1p, 2c, 3j-3m).

Subgroup B4: formed by the *Arctoa hyperborea*, *Oncophorus virens*, and *O. wahlenbergii*, which present anisomorphic spores with granulate sporoderm. Small to medium-sized spores (Table I) with bimodal spore size distribution (Fig. 6n-p). The sporoderm surface is ornamented with granula, which may be grouped or overlapped with different sizes and distributions (Figs. 1c, 1m, 1n, 2d, 2e, 2n, 2o).

Subgroup B5: formed exclusively by *Rhabdoweisia fugax*, it shows isomorphic spores and sporoderm surface with ornamentation processes other than granula. The spores are small in size (Table II) with unimodal spore size distribution (Fig. 6q). The sporoderm surface is ornamented by bacula which can be single or grouped, and exine shows exposed areas (Figs. 3n, 3o).

Subgroup B6: includes *Arctoa fulvella* and *Oreoweisia brasiliensis*, which present isomorphic spores and granulate sporoderm surface. The spores are small in size (Table I) with unimodal spore size distribution (Fig. 6r-s). The sporoderm surface is granulate, the granula can be grouped or overlapped with different sizes and distributions, and there are gemma in the apertural area. The exine is fully covered by the perine or shows small exposed areas (Figs. 1a, 1b, 2d, 2e, 2m).

Table III. Mean values of equatorial and polar diameters of heteropolar anisomorphic spores (in micrometers).

Species names	Smallest spores		Largest spores	
	Polar diameter	Equatorial diameter	Polar diameter	Equatorial diameter
Arctoa hyperborea	16.96	23.40	22.23	31.59
Cynodontium gracilescens	16.78	22.60	29.45	33.80
Cynodontium polycarpum	14.97	23.06	30.25	35.35
Cynodontium strumiferum	13.95	17.75	16.80	30.60
Cynodontium strumulosum	16.25	22.45	27.95	37.05
Cynodontium tenellum	13.78	21.45	17.94	29.25
Oncophorus virens	15.60	20.80	19.37	24.96
Oncophorus wahlenbergii	10.60	15.34	14.56	20.67

Table IV. Mean values of equatorial and polar diameters of heteropolar isomorphic spores (in micrometers).

Species names	Polar diameter	Equatorial diameter
Arctoa fulvella	13.55	16.75
Dicranoweisia crispula	11.05	15.08
Dicranoweisia cirrata	14.30	18.37
Oreas martiana	18.81	25.69
Oreoweisia brasiliensis	19.82	22.42
Oreoweisia laxiretis	16.36	23.47
Rhabdoweisia crispata	13.43	18.20
Rhabdoweisia fugax	10.92	15.60

Table V. Mean values of the sporoderm strata thickness and aperture diameter of anisomorphic spores (in micrometers).

Sporoderm strata	Aperture diameter			
Species names	Intine	Esclerine	Smallest spores	Largest spores
Actoa hyperborea	0.84	0.63	10.95	12.75
Cynodontium gracilescens	0.58	0.58	11.05	13.86
Cynodontium polycarpum	1.17	1.17	10.85	14.95
Cynodontium strumiferum	1.17	1.76	13.30	14.06
Cynodontium strumulosum	1.17	1.17	10.50	15.78
Cynodontium tenellum	1.17	1.17	11.65	15.06
Oncophorus virens	1.17	1.17	10.35	16.47
Oncophorus wahlenbergii	1.17	1.17	6.68	9.58

Table VI. Mean values of the sporoderm strata thickness and aperture diameter of isomorphic spores (in micrometers).

Sporoderm strata	Aperture diameter		
Species names	**Intine**	**Esclerine**	
Arctoa fulvella	1.05	1.17	6.00
Dicranoweisa crispula	0.99	1.17	5.96
Dicranoweisa cirrata	1.17	1.17	9.82
Kiaeria falcata	0.58	0.58	not applicable
Kiaeria glacialis	0.58	1.17	not applicable
Kiaeria starkei	0.81	0.87	not applicable
Oreas martiana	1.05	1.11	7.58
Oreoweisia laxiretis	0.76	1.11	not applicable
Oreoweisia brasiliensis	0.78	0.87	11.70
Rhabdoweisia crispata	0.97	1.04	9.2
Rhabdoweisia fugax	1.17	0.58	8.7

DISCUSSION

Anisospory has been described for several non-related families of mosses (Alfayate et al. 2013, Ernst-Schwarzenbach 1944, Mogesen 1981, Rodrigues & Luizi-Ponzo 2015, Vitt 1968), being reported here for the first time for Oncophoraceae. The anisosporic species of this family are included in three genera: *Arctoa*, *Cynodontium* and *Oncophorus*.

One species in *Arctoa* presented isomorphic spores (*A. fulvella)*, and the other anisomorphic spores (*A. hyperborea*). Frisvoll (1978) says that *A. fulvella* presents spores with larger diameter between 14-24µm, and Ochyra & Buck (2003) cite spores as globose, with a rough surface and larger diameter between 18-22 µm. Newmaster (2017) says that *A. fulvella* spores have diameter between 16-28 µm and *A. hyperborea* about 16-30 µm; these measurements are close to those found in this study.

Newmaster (2017) indicates *Cynodontium* spores measuring about 10µm to 25µm, and describes them as smooth to baculate, while *Oncophorus* spores are described by him as gently rough, measuring about 14µm to 25µm. These measurements are compatible with those found herein to the "smallest spores" of these genera; however, Newmaster (2017) does not mention the occurrence of anisospory.

Our results demonstrate that the species of *Cynodontium* studied are included in a single morphological type of spores, supporting the taxonomical interpetation of these species. However, species of *Oncophorus* were grouped in the same palynological type, but together with a species of *Arctoa* (*A. hyperborea*), showing the morphological complexity of these species.

Luizi-Ponzo & Barth (1999) described *Oreoweisia brasiliensis* spores. They indicated the measurements of the spore diameter as being about 20.80 µm to 30.40 µm, while the mean was 24.10 µm ± 0.40 µm. The spore size range is larger than that found in this study (18.20 µm - 28.60 µm), but the mean is close (24.20 µm ± 0.38 µm), while the granulate surface and the apertural area fit in both studies.

Tan & Schofield (1980), Schofield (2017) and Weber (2017) reported the spores of *Dicranoweisia* and *Oreas martitana* employing

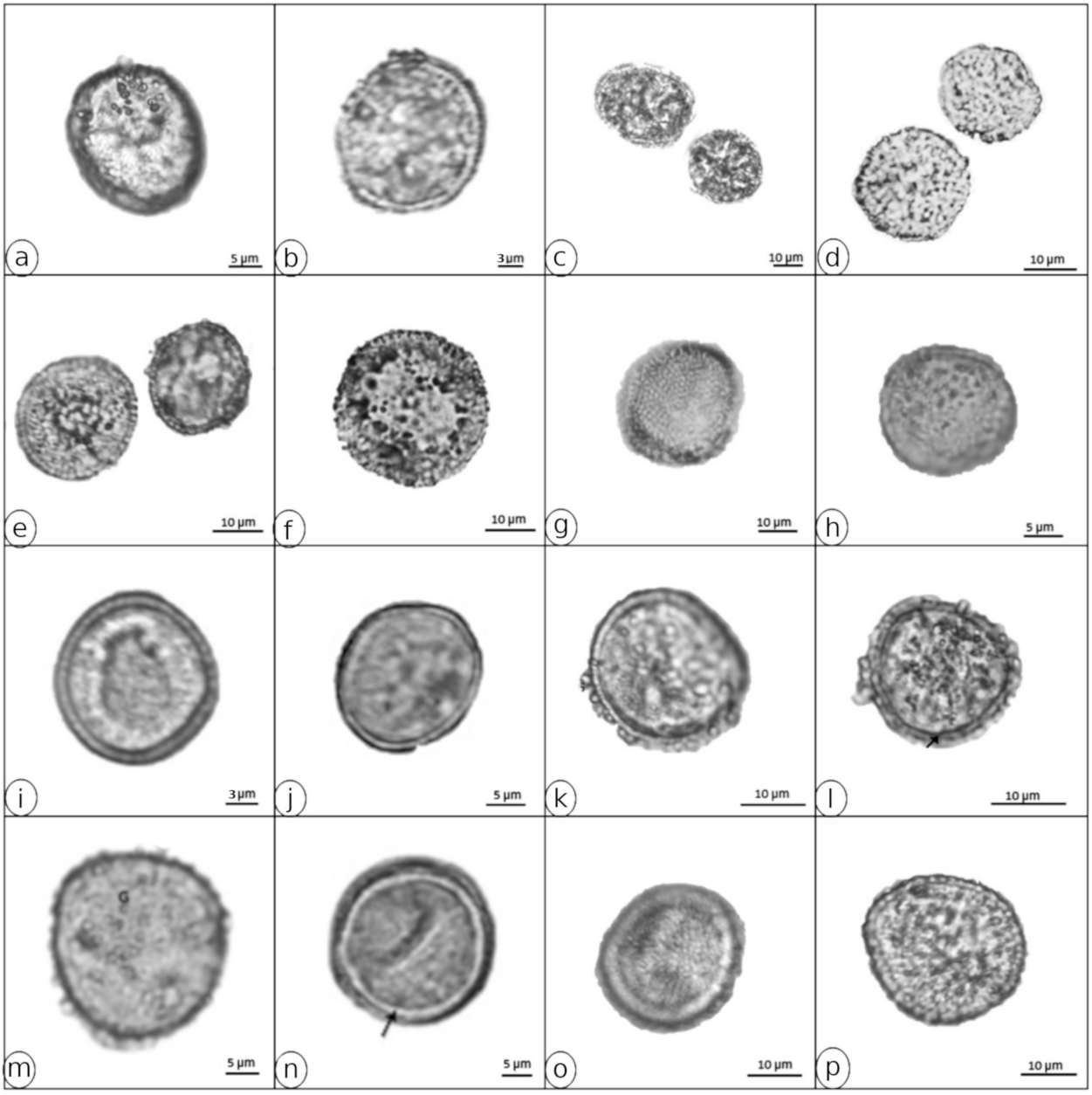

Figure 1. Spores photomicrographs of Oncophoraceae species. a-b. *Arctoa fulvella*. a, distal surface view. b. sporoderm stratification. c. *Arctoa hyperborea*, distal surface view of two spores. d. *Cynodontium gracilescens*, sporoderm of two spores. e. *Cynodontium strumiferum*, surface view (left) and sporoderm stratification (right). f. *Cynodontium strumulosum*, sporoderm view. g. *Cynodontium tenellum*, distal surface view. h. *Dicranoweisia cirrata*, sporoderm stratification. i. *Kiaeria falcata*, proximal surface view. j. *Kiaeria starkei*, sporoderm stratification. k. *Oreoweisia laxiretis*, sporoderm stratification. l. *Oreas martiana*, sporoderm stratification. m. *Oncophorus virens*, sporoderm stratification. n. *Oncophorus wahlenbergii*, sporoderm stratification. o. *Oreoweisia brasiliensis*, distal surface view. p. *Rhabdoweisia crispata,* sporoderm stratification.

a different terminology, but similarities are observed with the specimens examined here. However, for *O. martiana*, Weber (2017) cites spores of about 16 µm; this is quite different from those spores reported herein, as we observed a higher amplitude and different mean size.

Newmaster (2017) characterized the spores of *Kiaeria* as spherical, measuring about 14µm

and 24µm; these values are near to those observed herein. All *Kiaeria* species studied were grouped in the same morphological type of spores, corroborating the their generic circumscription.

While studying Amphidiaceae spores, Passarella & Luizi-Ponzo (2019) considered them to be isomorphic, small in size and with a strong heteropolar condition, in which the distal faces of the spores are perforated, and the proximal faces exhibited an apertural area surrouded by gemma and rugulae connected. Our results demonstrated that these conditions are not found in the spores of Oncophoraceae, favoring the separation of families, as proposed by Frey & Stech (2009).

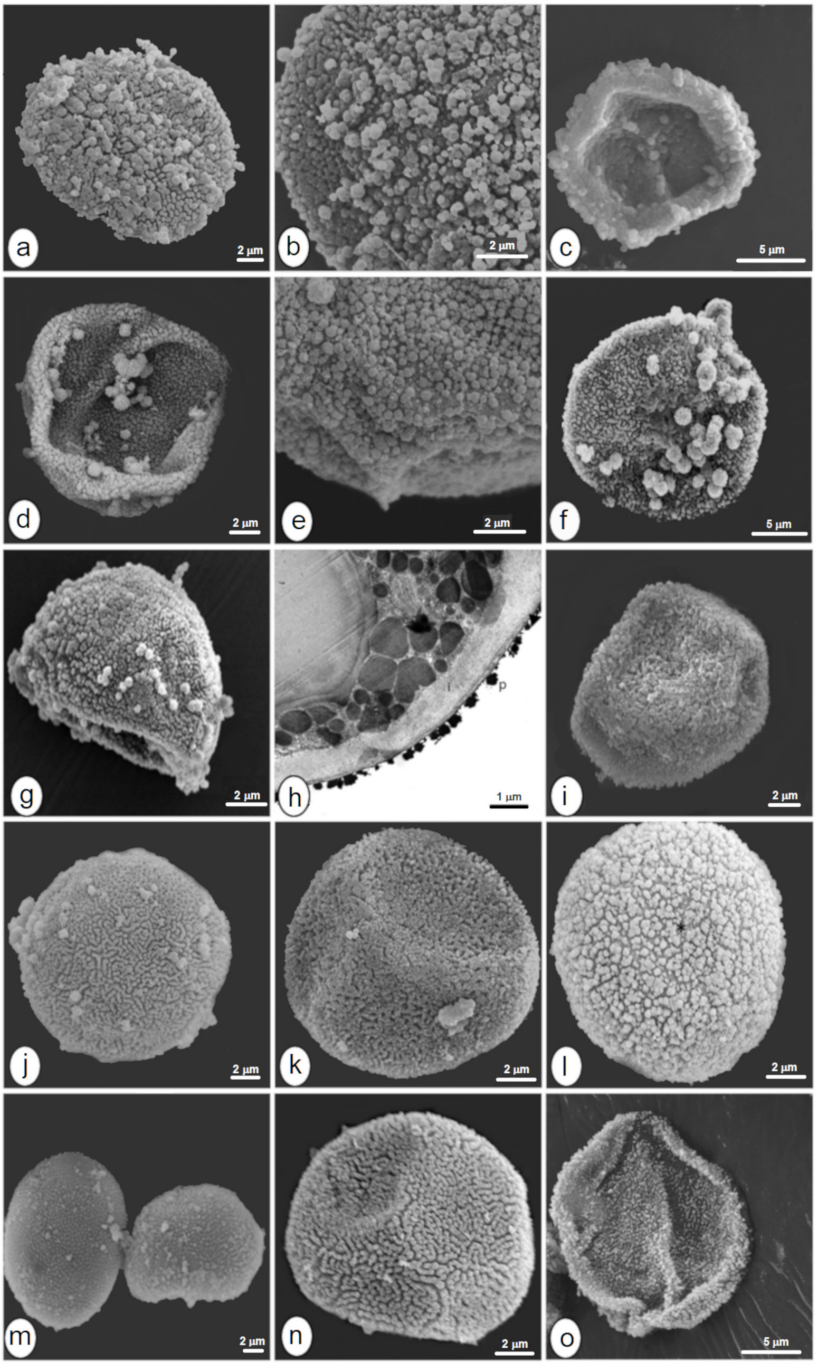

Figure 2. Spores electronmicrographs of Oncophoraceae species. a-b. *Oreoweisia laxiretis.* a. equatorial view. b. detail of surface. c. *Oreas martiana*, proximal view. d-e. *Arctoa fulvella*. d. proximal view. e. detail of surface. f-h. *Arctoa hyperborea*. f. distal view. g. equatorial view. h. sporoderm stratification. i. *Kiaeria falcata*, distal view. j-k. *Kiaeria glacialis*. j. distal view. k. detail of surface view. l. *Kiaeria starkei*, distal view. m. *Oreoweisia brasiliensis*, distal view (left), and equatorial view (right). n. *Oncophorus wahlenbergii*, distal view. o. *Oncophorus virens*, proximal view. Fig. 2h under TEM, the other: under SEM.

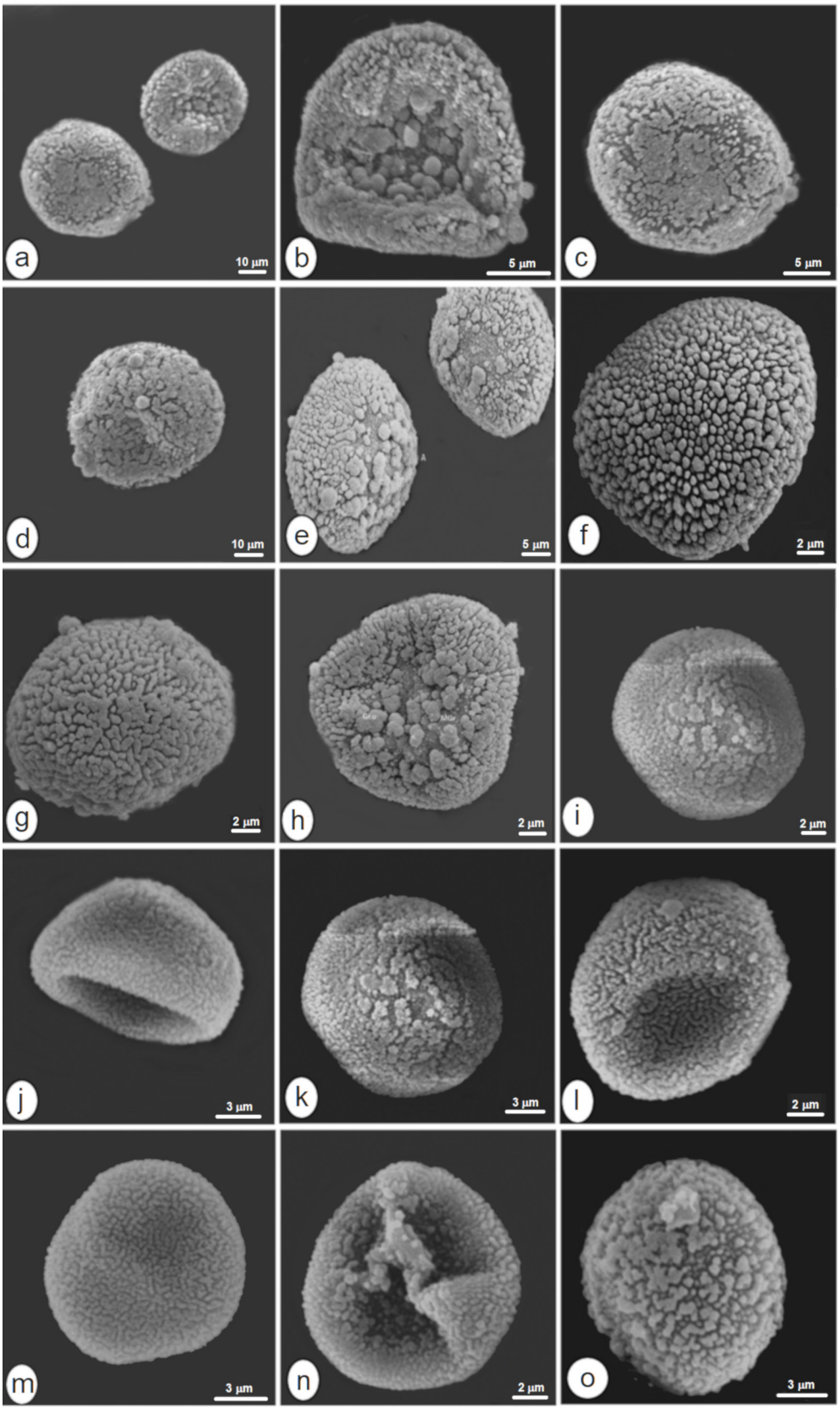

Figure 3. Spores electronmicrographs of Oncophoraceae species, under TEM. a-d. *Cynodontium polycarpon*. a. distal view (left) and proximal view (right) of spores. b. detail of spore proximal view. c. distal view. d. subproximal view. e-f. *Cynodontium strumiferum*. e. subequatorial view (left) and subproximal view (right). f. distal view. g-h. *Cynodontium tenellum*. g. distal view. h. proximal view. i-m. *Dicranoweisia cirrata*. i. distal view. j. equatorial view. k. proximal view. l. subequatorial view. m. distal view. n-o. *Rhabdoweisia fugax*. n. proximal view. o. distal view.

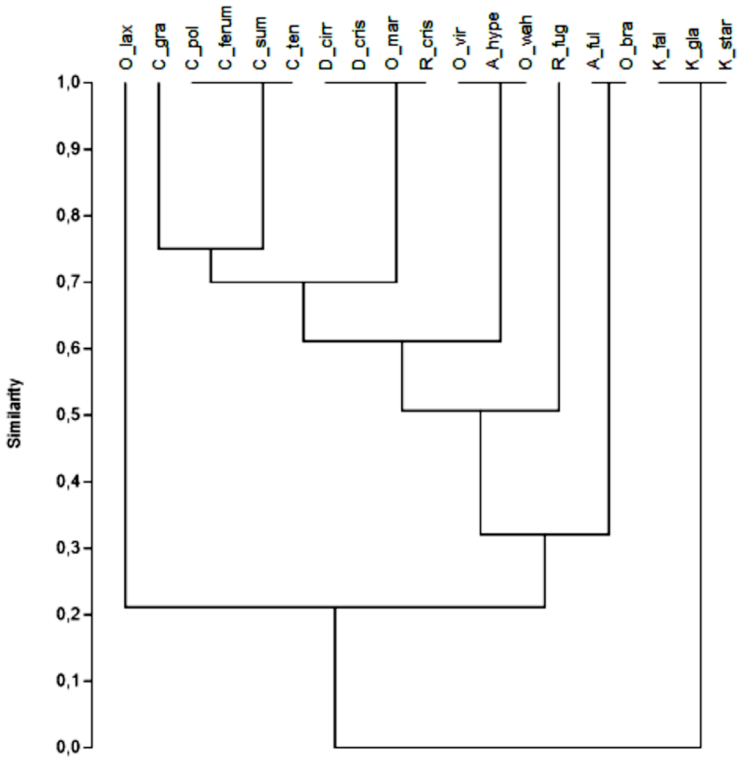

Figure 4. Dendrogram resulting from the Cluster Analysis.
Legend: O_laxi: ***Oreoweisia laxiretis*****;** **C_gra:** ***Cynodontium gracilescens*****;** **C_pol:** ***Cynodontium polycarpum*****;** **C_ferum:** ***Cynodontium strumiferum*****;** **C_strum:** ***Cynodontium strumulosum*****;** **C_ten:** ***Cynodontium tenellum*****;** **D_cir:** ***Dicranoweisia cirrata*****;** **D_cris:** ***Dicranoweisia crispula*****;** **O_mar:** ***Oreas martiana*****;** **R_cris:** ***Rhabdoweisia crispata*****;** **O-vir:** ***Oncophorus virens*****;** **A_hype:** ***Arctoa hyperborea*****;** **O_wah:** ***Oncophorus wahlenbergii*****;** **R_fug:** ***Rhabdoweisia fugax;*** **A_ful:** ***Arctoa fulvella*****;** **O_bra:** ***Oreoweisia brasiliensis*****;** **K_fal:** ***Kiaeria falcata*****;** **K_glac:** ***Kiaeria glacialis*****;** **K_star:** ***Kiaeria starkei.***

Table VII. Palynological characteristics employed on Cluster Analysis.

Species	Ornamentation	Sporoderm thickness	Polarity	Size condition	Apertural area
Arctoa fulvella	Granulate	2.22 µm	Heteropolar	Isomorphic	With delimitation
Arctoa hyperborea	Granulate	1.47 µm	Heteropolar	Anisomorphic	With delimitation
Cynodontium strumiferum	Baculate	2.93 µm	Heteropolar	Anisomorphic	With delimitation
Cynodontium strumulosum	Baculate	2.34 µm	Heteropolar	Anisomorphic	With delimitation
Cynodontium gracilescens	Baculate	1.16 µm	Heteropolar	Anisomorphic	With delimitation
Cynodontium polycarpum	Baculate	2.34 µm	Heteropolar	Anisomorphic	With delimitation
Cynodontium tenellum	Baculate	2.34 µm	Heteropolar	Anisomorphic	With delimitation
Dicranoweisia cirrata	Baculate	2.34 µm	Heteropolar	Isomorphic	With delimitation
Dicranoweisia crispula	Baculate	2.16 µm	Heteropolar	Isomorphic	With delimitation
Kiaeria falcata	Granulate	1.16 µm	Apolar	Isomorphic	Without delimitation
Kiaeria glacialis	Granulate	1.75 µm	Apolar	Isomorphic	Without delimitation
Kiaeria starkei	Granulate	1.68 µm	Apolar	Isomorphic	Without delimitation
Oreas martiana	Gemmae	2.16 µm	Heteropolar	Isomorphic	With delimitation
Oreoweisia brasiliensis	Granulate	1.65 µm	Heteropolar	Isomorphic	With delimitation
Oreoweisia laxiretis	Gemmae	1.87µm	Heteropolar	Isomorphic	Without delimitation
Oncophorus virens	Granulate	2.34 µm	Heteropolar	Anisomorphic	With delimitation
Oncophorus wahlenbergii	Granulate	2.34 µm	Heteropolar	Anisomorphic	With delimitation
Rhabdoweisia crispata	Baculate	2.01 µm	Heteropolar	Isomorphic	With delimitation
Rhabdoweisia fugax	Baculate	1.75 µm	Heteropolar	Isomorphic	With delimitation

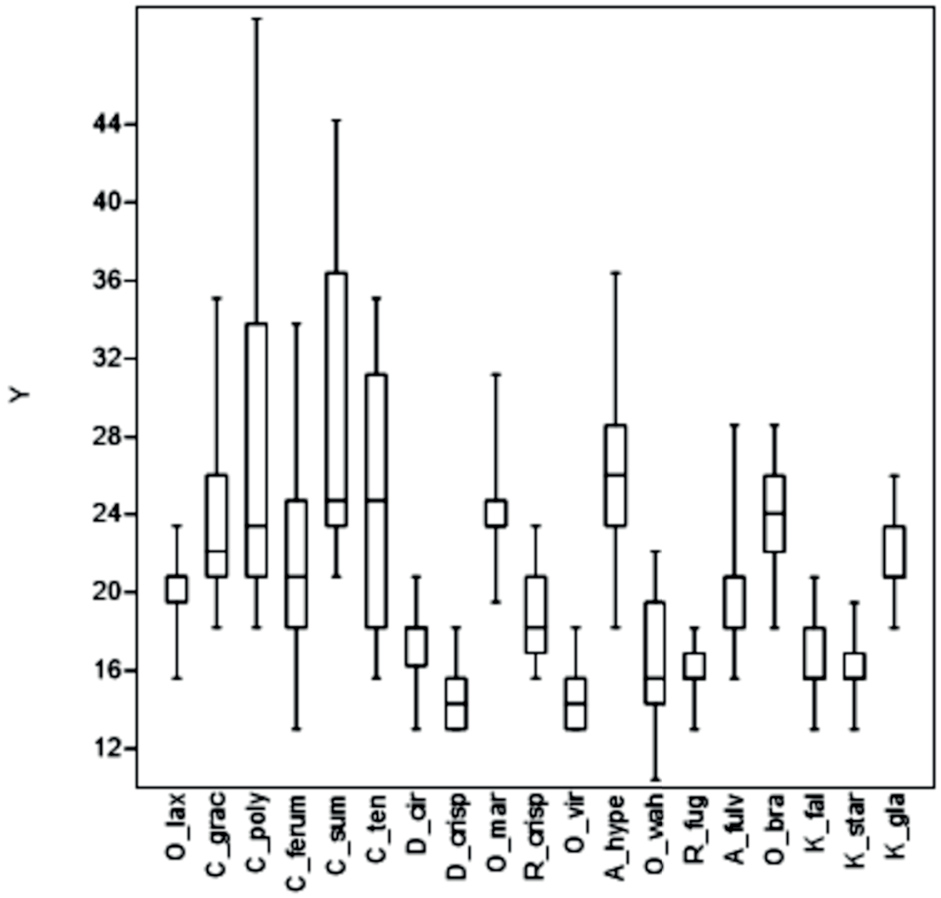

Figure 5. Graphic representation of the size measurements of the diameters of the spores (in micrometers). **Legend: O_laxi:** ***Oreoweisia laxiretis*****; C_gra:** ***Cynodontium gracilescens*****; C_pol:** ***Cynodontium polycarpum*****; C_ferum:** ***Cynodontium strumiferum*****; C_strum:** ***Cynodontium strumulosum*****; C_ten:** ***Cynodontium tenellum*****; D_cir:** ***Dicranoweisia cirrata*****; D_cris:** ***Dicranoweisia crispula*****; O_mar:** ***Oreas martiana*****; R_cris:** ***Rhabdoweisia crispata*****; O-vir:** ***Oncophorus virens*****; A_hype:** ***Arctoa hyperborea*****; O_wah:** ***Oncophorus wahlenbergii*****; R_fug:** ***Rhabdoweisia fugax;*** **A_ful:** ***Arctoa fulvella*****; O_bra:** ***Oreoweisia brasiliensis*****; K_fal:** ***Kiaeria falcata*****; K_glac:** ***Kiaeria glacialis*****; K_star:** ***Kiaeria starkei.***

CONCLUSION

Oncophoraceae species present small to medium spores with radial symmetry, subcircular amb, they are heteropolar or apolar. The sporoderm stratification includes perine, exine and intine. Eight species studied, representing three genera, present anisomorphic spores; this was not reported before, according to the studied literature.

The small size of the spores indicates the importance of SEM observations to refine the description of sporoderm of these species.

Kiaeria species: *K. falcata*, *K. glacialis* and *K. starkei* may be defined by the granulate surface of the spores; and the anisomorphic baculate spores of *Cynodontium* characterize the species of this genus.

Spore size, ornamentation and sporoderm stratification measurements vary between Oncophoraceae species, which allows us to say that the family is euripalynous. Despite the great morphological variability observed in the spores of the species of Oncophoraceae studied, their distinction from Amphidiaceae is here corroborated.

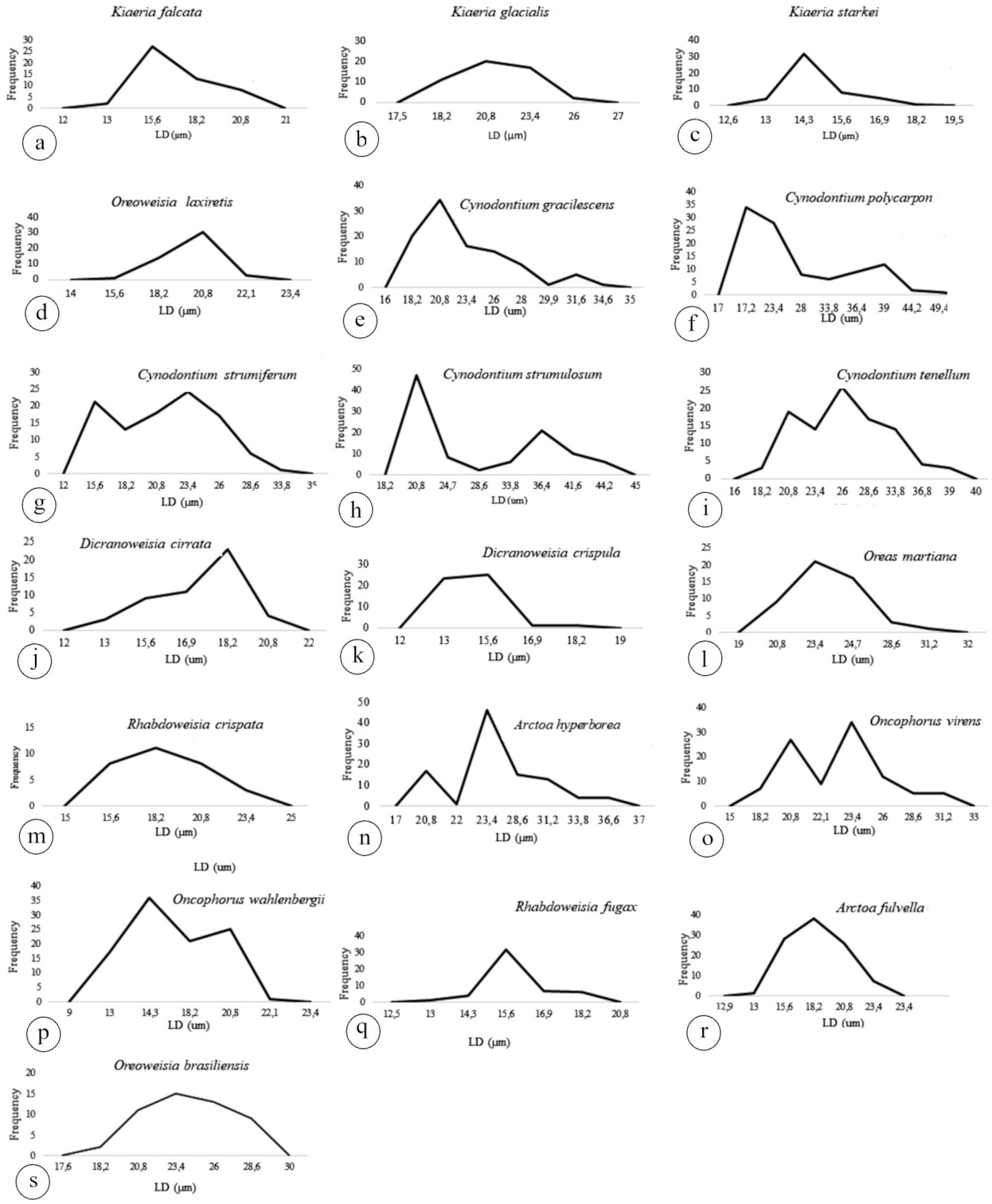

Figure 6. Line graphs representing the spore size frequency distribution of the species.

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Author contributions

APL-P - coordinator of the project in which this work is inserted, study design, obtaining the botanical material, supervision of the methodology employed, participation in obtaining the results and in the discussion.
MdAP - participation in the study design, preparation of botanical material for observation, measurement, statistical treatment, participation in the elaboration of results and discussion.