



Palynology of *Amphidium* Schimp. (Amphidiaceae M. Stech): can spore morphology circumscribe the genus?

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ABSTRACT

Amphidium Schimp. is characterized by cushion-forming erect primary stems, linear-lanceolate leaves, and gymnostome capsules. The phylogenetic position of *Amphidium* is uncertain, with the genus having been variously included in Zygodontaceae Schimp., Rhabdoweisiaceae Limpr., Orthotrichaceae Arn. and Amphidiaceae M. Stech. A palynological investigation was performed of the three species of the genus that occur in the Americas: *Amphidium lapponicum* (Hedw.) Schimp., *Amphidium mougeotii* (Bruch & Schimp.) Schimp., and *Amphidium tortuosum* (Hornsch.) Cufod. Spores were observed and measured for greatest diameter under light microscopy both before and after acetolysis. Non-acetolyzed spores were observed under scanning electron microscopy to assess surface ornamentation of the sporoderm. All spores observed were smaller than 20 µm and heteropolar, with surface ornamentation reflecting a combination of different elements, such as gemmae, rugulae and perforations. The palynological characteristics observed here suggest that the genus *Amphidium*, and thus its contained species, be placed in their own family.

Keywords: Amphidiaceae, bryophytes, haplolepidous moss, palynology, spores

Introduction

The moss genus *Amphidium* comprises plants that grow as cushions and possess an erect primary stem; linear-lanceolate leaves with rounded and papillose cells; a longitudinally-furrowed sporophyte with gymnostomous capsules that are emergent or exserted, and a cucullate calyptra (Rooy 1992; Frahm *et al.* 2000). The species are generally rupicolous, growing directly upon rocks or in rock cracks (Rooy 1992; Frahm *et al.* 2000; Sim-Sim *et al.* 2017).

Amphidium lapponicum and *Amphidium mougeotii* were first described by Schimper (1856) as belonging to the family Zygodontaceae due to their papillose leaf cells and cucullate calyptra. Other studies have suggested alternate systematic positions for this genus and even its species

circumscription. Brotherus (1924) included *Amphidium* in the subfamily Rhabdoweisioideae of Dicranaceae, which was followed by Walter (1983) and Allen (2002). Many authors have included *Amphidium* in Orthotrichaceae (Vitt 1984; 1994; Rooy 1992; Vitt *et al.* 1993; Gradstein *et al.* 2001) due to similarities with *Orthotrichum*, particularly regarding the development of young capsules, as pointed out by Lewinsky (1976). Ochyra *et al.* (2003) suggested that species of *Amphidium* be placed in the subfamily Amphidioideae of Dicranaceae.

Molecular studies have revealed that *Amphidium* belongs to a haplolepidous lineage (Goffinet *et al.* 1998; Stech 1999; Farge *et al.* 2000), but its relationships with other haplolepidous mosses, such as Dicranaceae and Oncophoraceae, remain uncertain (Farge *et al.* 2002; Tsubota *et al.* 2003; Hedderson *et al.* 2004; Stech 2004).

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Stech & Frey (2008) proposed the family Amphidiaceae to accommodate *Amphidium*, however, reviewing the phylogeny of haplolepidous mosses, Stech *et al.* (2012) revealed that Amphidiaceae was embedded within an unsupported clade, and thus the position of the family remains ambiguous.

Circumscribing the species of *Amphidium*, Frahm *et al.* (2000) proposed the recognition of: *Amphidium lapponicum*, *A. mougeotii* and *A. tortuosum*. Sim-Sim *et al.* (2017) reconstructed the phylogeny of this genus using morphological and anatomical characters, and indicated six species for the genus: *Amphidium lapponicum*, *A. mougeotii*, *A. tortuosum*, *A. californicum*, *A. curvipes*, and *A. asiaticum*.

Palynological studies dealing with bryophyte species have made important advances since the 1980s regarding the taxonomy, ecology, and phylogeny of the group (Mogensen 1981; 1983; Luiz-Ponzo & Barth 1998; 1999; Luiz-Ponzo & Melhem 2006a; b; Caldeira *et al.* 2006; 2009; 2013; Rocha *et al.* 2008; Savaroglu & Erkara 2008; Alfayate *et al.* 2013; Rodrigues & Luiz-Ponzo 2015; Silva-e-Costa *et al.* 2017). However, studies on *Amphidium* have focused mostly on morphological and molecular characters (Rooy 1992; Goffinet *et al.* 1998; Stech 1999; Farge *et al.* 2000; 2002; Frahm *et al.* 2000; Tsubota *et al.* 2003; Hedderson *et al.* 2004; Stech 2004; Stech & Frey 2008; Stech *et al.* 2012; Sim-Sim *et al.* 2017), with palynological information on its species remaining rare (Hirohama 1977) or only briefly summarized in some taxonomic studies (Rooy 1992; Gradstein *et al.* 2001; Allen 2002), in which they were described as “subrounded”, “small”, “apparently ornamented”, “slightly papillose” or “having a smooth sporoderm”.

The present study aimed to investigate the palynology of the three species of *Amphidium* that occur in the Americas, as recognized by Frahm *et al.* (2000) — *Amphidium lapponicum*, *Amphidium mougeotii*, and *Amphidium tortuosum* — in order to evaluate the importance of spores to the taxonomic circumscription of *Amphidium* and to compare the spore morphology of this genus to that of other haplolepidous mosses.

Materials and methods

The following specimens were examined:

Amphidium lapponicum (Hedw.) Schimp.: Finland: Carelia, 06/ VII/ 1904. E. Bauer 228 (UB); Sweden: Hälsingland, 26/ VI/ 2008. L. Hedenas *et al.*, 27 (UB); Germany: Gotha: Buchberg, IX/ 1885, Schmith s/n° (R 80442); Canada: Ontario: Nipissing District, 29/ VII/1938, R.F. Cain, 243 (CANM). *Amphidium mougeotii* (Bruch & Schimp.) Schimp. United States of America: Washington: Pierce and Lewis County, Rainier Mountain National Park, Denman Falls, 23/ VIII/ 1963, R. R. Ireland 8326 (CANM); United States of America: Washington: Pierce and Lewis County, Rainier Mountain National Park, 22/ VIII/ 1963, R.R. Ireland & E. Lawton 8263 (CANM); Bolivia: La Paz, Murillo Province, M.

Lewis 88005 (SP). *Amphidium tortuosum* (Hornsch.) Cufod. Guatemala: Chiapas: Union Juarez, D.E. Breedlove 29357 (SP); United States of America: Hawaii: Haleakala National Park, Leg.: W. J. Hoe 35070 (SP).

Spores were observed under light microscopy (LM) and scanning electron microscopy (SEM). Spores for LM were prepared and analyzed following the methods of Wodehouse (1935) and Erdtman (1960), as modified by Luiz-Ponzo & Melhem (2006a) for bryophytes. Spores for SEM analysis were dispersed upon stubs covered with double-sided tape and coated with a 20-µm layer of gold.

Spore largest diameter was measured under LM with an ocular micrometer. A single sample was established as the standard for each species, while other samples were used for comparison. Fifty acetolyzed spores from three different microscope slides were measured for the standard material, while 30 acetolyzed spores from three different microscope slides were measured for the comparative material. Measurements were taken in polar view. Arithmetic mean (X), standard deviation (S), standard error (Sx), coefficient of variability/variation (CV %), and the 95 % confidence interval (CI), as well as minimum and maximum spore size (Xmin–Xmax), are reported for each of the analyzed samples. Mean polar diameter and equatorial diameter were obtained by measuring, always in equatorial view, 30 randomly selected acetolyzed spores. Since data for maximum diameter, polar diameter and equatorial diameter did not meet the assumptions of normality, they were analyzed using the non-parametric Kruskal Wallis test. Dunnet's a posteriori test was then used to test differences between standard and comparative material for each species and among standard material of all three species. Statistical analyses were performed in R version 3.4.2 (2017-09-28) (R Core Team 2017).

Due to the thinness of the perine and exine, they were measured together as the sclerine (Luiz-Ponzo & Barth 1998; 1999). Thus, the layers that compose the sporoderm — sclerine and intine — were measured from 10 randomly selected spores, which were prepared following the method of Wodehouse (1935) (with modifications by Luiz-Ponzo & Melhem 2006a), and arithmetic means calculated. Spore descriptions follow Punt *et al.* (2007) for terminology and Erdtman (1952) for spore size classes.

Results

The spores of species of *Amphidium* are small, heteropolar, isomorphic, and have a subcircular amb (Tab. 1, Fig. 1). The sporoderm comprises the intine and the sclerine (exine plus perine) and exhibits various ornamentation elements. These elements are similar to gemmae and are connected with each other and associated with thick rugulae on the proximal spore face; the sporoderm is perforated on the distal spore face (Fig. 2), while the perine entirely covers the exine. The apertural region is highlighted by a differentiated pattern of

ornamentation comprising connected gemmae associated with thick rugulae and a delicate sulcus. The three analyzed species of the genus *Amphidium* possess similar sporoderm ornamentation (Fig. 2), while they vary in morphometric characteristics (Tabs. 1-4), as explained below.

The spores of *Amphidium lapponicum* had the lowest mean largest diameter (Tab. 1). In addition, the mean largest diameters for the two comparative samples [Schmith s/n° (R 80442) and R. F. Cain 243 (CANM)] did not fall within the 95 % confidence interval of the standard material (Tab. 1), but were not significantly different ($p = 0.17$ and $p = 0.7$, respectively). The mean polar diameter for the species was $9.54 \mu\text{m}$ while the mean equatorial diameter was $13.08 \mu\text{m}$.

For spores of *Amphidium mougeotii*, the mean largest diameter of the comparative sample M. Lewis 88005 (SP) did not fall within the 95 % confidence interval of the standard material, but was not significantly different ($p = 0.48$). The mean polar diameter for the species was $10.74 \mu\text{m}$ while the mean equatorial diameter as $14.95 \mu\text{m}$. The thicknesses of the sporoderm layers of this species were similar to that of the sporoderm of *A. lapponicum* (Tab. 2).

Spores of the *Amphidium tortuosum* had the greatest largest diameter among the studied species (Tab. 1). The largest diameter of the comparative sample W. J. Hoe 35070 did not fall within the 95 % confidence interval of the standard material, and was significantly different

Table 1. Morphometric data of largest diameter of the spores from *Amphidium* Schimp. species. Data presented in micrometers (*standard material; other data: comparison material). X_{\min} - X_{\max} = Sample minimum and maximum values; \bar{X} = arithmetic mean; S_x = standard deviation; S = standard error; CI = confidence interval; VC = variation coefficient.

	X_{\min} - X_{\max}	$\bar{X} \pm S_x$	S	IC 95%	CV
<i>A. lapponicum</i> (Hedw.) Schimp.					
E. Bauer, 228* (UB)	10.40-14.30	12.53 ± 0.14	1.02	12.14- 12.91	8.14
L. Hedenas et. al, 27 (UB)	10.40-15.60	12.22 ± 0.27	1.50	11.44- 12.95	12.27
Schimit, s/n° (R)	10.40-16.90	13.47 ± 0.34	1.88	12.55 - 14.38	13.96
R. F. Cain, 243 (CANM)	11.70-15.60	14.04 ± 0.21	1.20	13.45-14.62	8.55
<i>A. mougeotii</i> (Bruch & Schimp.) Schimp.					
R. R. Ireland, 8362* (CANM)	10.40-18.20	14.63 ± 0.20	1.45	14.08 - 15.17	9.91
R. R. Ireland, 8263 (CANM)	10.40-18.20	15.03 ± 0.29	1.58	14.23 - 15.82	10.51
<i>A. tortuosum</i> (Hornsch.) Cufod.					
D.E. Breedlove, 29347* (SP)	13.65-20.80	17.16 ± 0.24	1.70	16.51- 17.80	10.51
Leg.: W. J. Hoe, 35070 (SP)	15.60- 23.4	19.29 ± 0.39	2.10	18.23 - 20.34	10.89

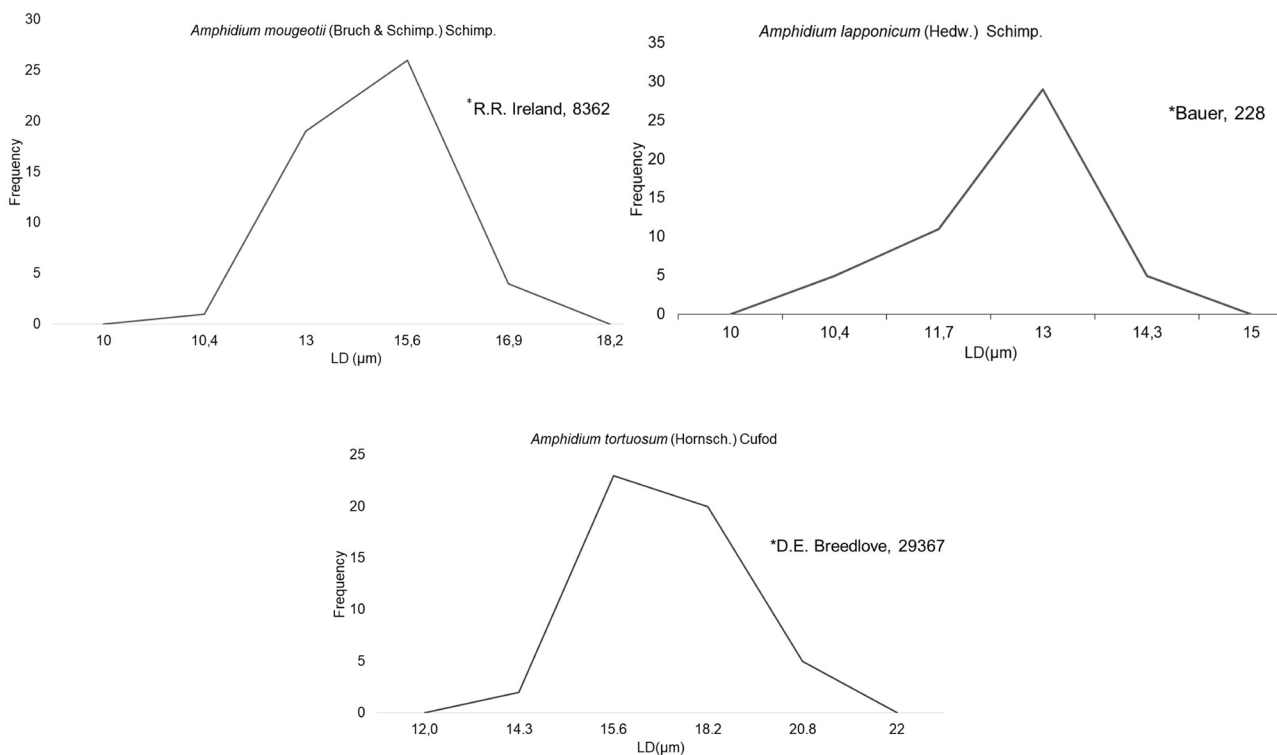


Figure 1. Line graphs representing the size distribution of the spores of the studied species of *Amphidium* Schimp.



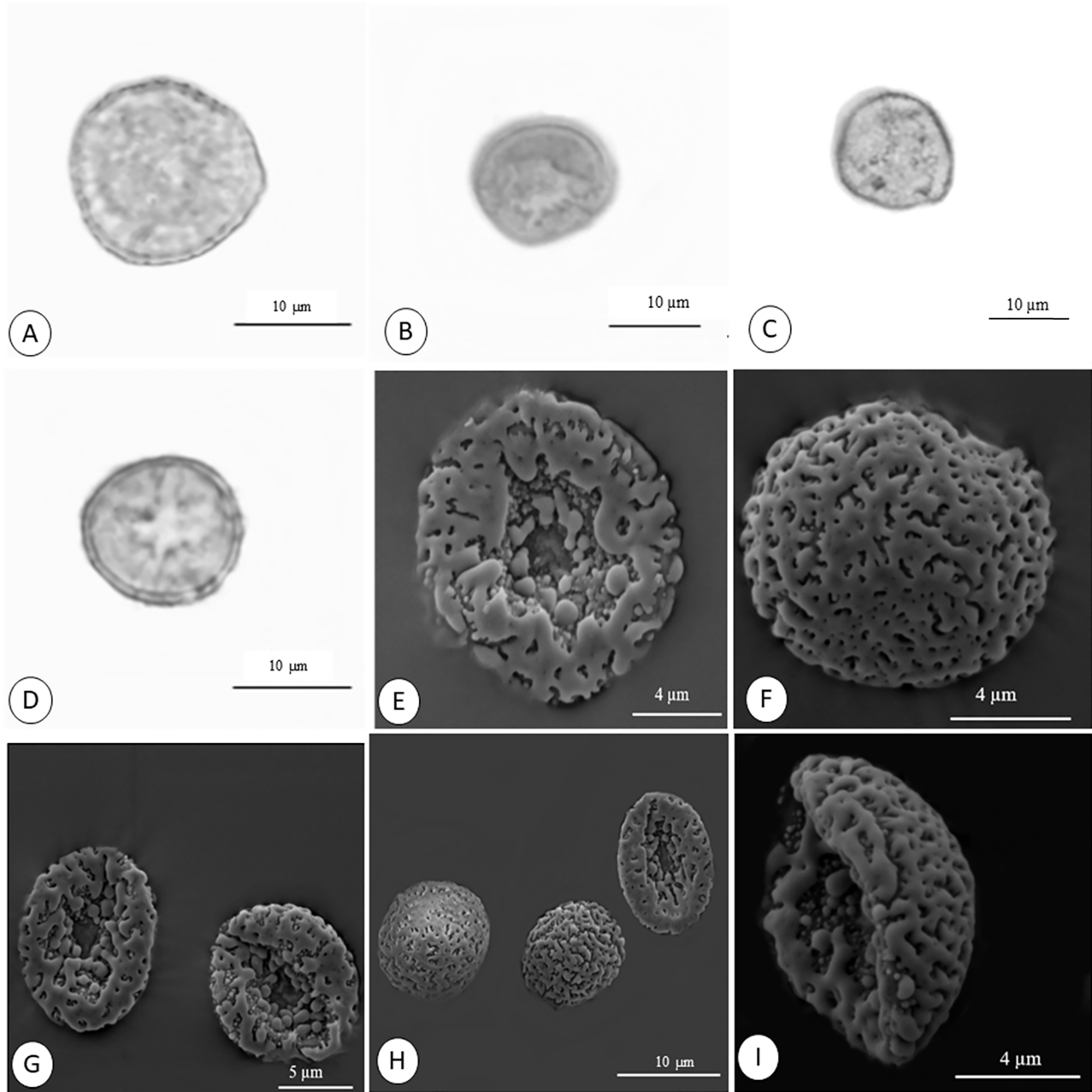


Figure 2. Spores of *Amphidium* Schimp species under light and scanning electronic microscopy. A, E - I: *A. lapponicum* (Hedw.) Schimp.; B and D: *A. mougeotii* (Bruch & Schimp.) Schimp.; C: *A. tortuosum* (Hornsch.) Cufod. A, B, C and D: light microscopy images; E, F, G, H and I: scanning electronic microscopy images.

Table 2. Mean values of sporoderm layers thickness (in µm) of spores of *Amphidium* Schimp., and mean size value of aperture area (in µm) (*standard material).

	Intina	Esclerina	Area apertural
<i>A. lapponicum</i> (Hedw.) Schimp. E. Bauer, 228* (UB)	1.12	1.12	7.37
<i>A. mougeotii</i> (Bruch & Schimp.) Schimp. R. R. Ireland, 8362* (CANM)	1.11	1.17	11.52
<i>A. tortuosum</i> (Hornsch.) Cufod. D.E. Breedlove, 29347* (SP)	0.61	1.17	10.27

Table 3. P values resulting from the Dunnet test for the measurements of polar diameter (PD), equatorial diameter (ED) and aperture regions (AR) of the three species of *Amphidium* Schimp. analyzed.

	<i>A. lapponicum</i> (Hedw.) Schimp.			<i>A. mougeotii</i> (Bruch & Schimp.) Schimp.		
	PD	ED	AR	PD	ED	AR
<i>A. mougeotii</i> (Bruch & Schimp.) Schimp.	0.0017	9.5 * 10 ⁻⁶	0.00028			
<i>A. tortuosum</i> (Hornsch.) Cufod.	1.6* 10 ⁻⁵	9.5 * 10 ⁻⁶	0.00031	7.1 * 10 ⁻⁶	9.5 * 10 ⁻⁶	0.00241

($p < 0.001$) (Tab. 1). The mean polar diameter for this species was 16.10 μm while the mean equatorial diameter was 18.54 μm . The intine of the sporoderm of *A. tortuosum* was found to be thinner than the strata (sclerine and intine) of the other species (Tab. 2).

Significant differences were found for mean aperture region size ($p < 0.0001$), and mean polar ($p < 0.0001$) and equatorial ($p < 0.0001$) diameters (Tab. 3). Despite overlap in the largest diameters of the three studied species (Fig. 1), they differed significantly ($p < 0.0001$) (Tab. 4).

Table 4. P values resulting from the Dunnett test for the largest diameter of the three *Amphidium* Schimp. species analyzed

	<i>A. lapponicum</i> (Hedw.) Schimp.	<i>A. mougeotti</i> (Bruch & Schimp.) Schimp.
<i>A. mougeotti</i> (Bruch & Schimp.) Schimp.	6.2×10^{-11}	
<i>A. tortuosum</i> (Hornsch.) Cufod.	2×10^{-16}	1.1×10^{-10}

Discussion

Spore size for the genus *Amphidium* is unimodally distributed, and there is an absence of aborted spores. This, according to Mogensen (1981), is indicative of isomorphic spores.

The coefficient of variability found here for spore size is comparable to that reported by previous studies of bryophyte spores, which were around 10 % (Luizi-Ponzo & Barth 1998; Caldeira *et al.* 2009), due to the size amplitude observed in bryophyte spores.

Few studies have provided palynological observations for *Amphidium*, and those that did only provided superficial information on spore morphology. Hirohama (1977) studied the spores of a variety of different species including two species of *Amphidium*, using SEM and recognized distinct patterns of spore ornamentation among the genera analyzed. Gradstein *et al.* (2001) cited the spores of some species of *Amphidium* as being ‘apparently ornate’, while Allen (2002) described them as being ‘slightly papillose’. van Rooy (1992) reported the spores of *A. lapponicum* and *A. tortuosum* as being small, ‘sub-rounded’, and with largest diameters of around 11-15 μm and 12-22 μm , respectively, which are consistent with the results of the present study.

Sim-Sim *et al.* (2017) described the spores of *Amphidium asiaticum*, and reported a largest diameter of 14 μm , which is smaller than that found for the species of the present study. Sim-Sim *et al.* (2017) also reported *A. asiaticum* as having a smooth sporoderm, however, this may be a result of their observations being restricted to LM, which precludes a more complete sporoderm analysis.

The ornamentation observed for the spores of the species of the present study was found to be similar to that reported

for *Zygodon obtusifolius* (Luizi-Ponzo 2001), a species of Orthotrichaceae, which is a diplolepidous moss lineage (Goffinet *et al.* 1998). Molecular analyses have suggested that the group formed by Orthotrichales, Splachnales and Bryales *sensu lato* is monophyletic and the sister-group of haplolepidous mosses (Goffinet *et al.* 1998).

The spores of *Amphidium* are morphologically distinct from the spores of the other genera of Rhabdoweisiaceae, such as *Arctoa*, *Cynodontium*, *Oreoweisia*, *Oncophorus*, among others (Passarella 2018), and even from other haplolepidous moss taxa, such as *Holomitrium*, *Campylopus*, *Dicranella*, *Eobrychium* and *Trematodon*, among others (Luizi-Ponzo & Barth 1998; 1999).

Thus, the palynological descriptions presented here provide important information for future studies dealing with the phylogeny of haplolepidous mosses, which to date have remained inconclusive about the placement of *Amphidium* (Farge *et al.* 2002; Tsubota *et al.* 2003; Hedderson *et al.* 2004; Stech 2004; Stech *et al.* 2012).

Our results support the taxonomical circumscription proposed by Stech and Frey (2008), who proposed the family Amphidiaceae to segregate *Amphidium*.

Conclusion

Species of *Amphidium* possess palynological characters that distinguish them from other taxa of Rhabdoweisiaceae, and from the spores of other species of the haplolepidous lineage. The spores are heteropolar with an apertural area on the proximal face that is clearly distinguishable by its remarkable ornamentation: connected gemmae associated with thick rugulae. The distal face, on the other hand, possesses a perforated sporoderm. The results of the present palynological study support the segregation of *Amphidium* in its own family.

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