http://dergipark.org.tr/tr/pub/anatolianbryology

DOI: 10.26672/anatolianbryology.1566801

Anatolian Bryology
Anadolu Briyoloji Dergisi
Research Article
e-ISSN:2458-8474
Online

The Investigation of Comparative Spore Morphologies of Acrocarpous and Pleurocarpous Two Mosses (Bryophyta)

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Received: 14 October 2024 **Revised: 31 October 2024** **Accepted: 01 November 2024**

Abstract

Bryophyta members in the subkingdom Bryobiotina are distributed in a wide variety of habitats. Mosses are morphologically divided into two large groups: acrocarpous and pleurocarpous. Acrocarpic species have arid character and pleurocarpic species are distributed in more moist regions. The spores of the pleurocarpous *Brachythecium salebrosum* (Hoffm. ex F. Weber & D. Mohr) Schimp. and the acrocarpous *Crossidium squamiferum* var. *pottioideum* (De Not.) Mönk. were examined in comparison in this study. Spore slides were prepared using both Erdtman (acetolysis) and Wodehouse methods and examined under a light microscope (LM). As a result of the analyses, it was found that the spores of *C. squamiferum* var. *pottioideum* were oblate in both methods, while the spores of *B. salebrosum* were suboblate in the acetolysis method and oblate in the Wodehouse method. Spores of both taxa are classified as small spores. Furthermore, the equatorial axis is longer than the polar axis in the spores of both taxa and the thicknesses of the intine layer of the spores are almost identical at 0.50 µm (*B. salebrosum*) and 0.53 µm (*C. squamiferum* var. *pottioideum*). In addition, the thickness of the sclerine of *B. salebrosum* spores was about 0.70 µm in both methods, while it was 0.56 µm in acetolysed spores of *C. squamiferum* var. *pottioideum* and 0.78 µm in Wodehouse treated spores. Both taxa have monolete and trilete spores. On the other hand, SEM examinations revealed that *B. salebrosum* has gemmate ornamentation, while *C. squamiferum* var. *pottioideum* has verrucate ornamentation. The findings obtained as a result of the studies helped to reveal the differences between the spores of taxa in different morphological groups and brought a different perspective in their ecological evaluation.

Keywords: Acrocarpous, Pleurocarpous, Mosses, Spore morphology

Akrokarp ve Pleurokarp İki Karayosunun (Bryophyta) Karşılaştırmalı Spor Morfolojilerinin İncelenmesi

Öz

Bryobiotina alt alemindeki Bryophyta üyeleri çok çeşitli habitatlarda dağılım gösterir. Karayosunları morfolojik olarak iki büyük gruba ayrılır: akrokarp ve pleurokarp. Akrokarpik türler kurak karaktere sahipken, pleurokarpik türler daha nemli bölgelerde yayılış gösterir. Bu çalışmada pleurokarp *Brachythecium salebrosum* (Hoffm. ex F. Weber & D. Mohr) Schimp. ve akrokarp *Crossidium squamiferum* var. *pottioideum* (De Not.) Mönk. sporları karşılaştırmalı olarak incelenmiştir. Spor preparatları hem Erdtman (asetoliz) hem de Wodehouse yöntemleri kullanılarak hazırlanmış ve ışık mikroskobu (IM) altında incelenmiştir. Analizler sonucunda, *C. squamiferum* var. *pottioideum* sporlarının her iki yöntemde de oblat olduğu, *B. salebrosum* sporlarının ise asetoliz yönteminde suboblat, Wodehouse yönteminde ise oblat olduğu tespit edilmiştir. Her iki taksonun sporları da küçük sporlar olarak sınıflandırılır. Ayrıca, her iki taksonun sporlarında ekvatoral eksen polar eksenden daha uzundur ve sporların intin tabakasının kalınlıkları 0,50 µm (*B. salebrosum*) ve 0,53 µm (*C. squamiferum* var. *pottioideum*) ile neredeyse aynıdır. Buna ek olarak, *B. salebrosum* sporlarının sklerin kalınlığı her iki yöntemde de yaklaşık 0,70 µm iken, *C. squamiferum* var. *pottioideum*'un asetolize sporlarında 0,56 µm ve Wodehouse yöntemi uygulanmış sporlarda ise 0,78 µm'dir. Her iki takson da monolet ve trilet sporlara sahiptir. Diğer yandan, SEM incelemeleri *B. salebrosum*'un gemmat ornamentasyona sahip olduğunu, *C. squamiferum* var. *pottioideum*'un ise verrukat ornamentasyona sahip olduğunu ortaya koymuştur. Çalışmalar sonucunda elde edilen bulgular, farklı morfolojik gruplarda yer alan taksonların sporları arasındaki farklılıkların ortaya konmasına yardımcı olmuş ve ekolojik değerlendirmelerinde farklı bir bakış açısı getirmiştir.

Anahtar kelimeler: Akrokarp, Pleurokarp, Karayosunları, Spor morfolojisi

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To cite this article: *Aslan Ergenekon Z. Ay E. Ezer T. 2024. The Investigation of Comparative Spore Morphologies of Acrocarpous and Pleurocarpous Two Mosses (Bryophyta). Anatolian Bryology. 10:2, 110-119.*

1. Introduction

The second largest plant group in terms of the number of species after closed-seeded plants are the bryophytes, the ancestors of terrestrial plants. There are about 20.000 species of bryophytes worldwide (URL1). Within the subkingdom Bryobiotina, there are 3 divisions: hornworts (Anthocerotophyta), liverworts (Marchantiophyta) and mosses (Bryophyta) (Glime, 2017). Bryophytes can be found in a wide variety of climates where sufficient moisture is provided to sustain their life. They are important parts of many ecosystems, from tropical to subarctic and subantarctic areas (Walsh et al., 2024).

Bryophytes have a haplodiplontic life cycle, producing diploid (2n) sporophytes and haploid (n) gametophytes (Simpson, 2012). Gametophytic and sporophytic characters have an important place in the taxonomy of bryophytes. In taxonomic classification, micro-morphological characteristics as well as macro-morphological characteristics are used. These plants reproduce with small unicellular spores and their spore morphology is of palaeobotanical, taxonomic and ecological importance. Most bryophyte spores are 10-50 μm in diameter, but there are exceptions where spores can be larger (250 μm-some *Archidium* Brid. species) or smaller (7 μm-some *Grimmia* Hedw. species) depending on the genus (Khoshravesh and Kazempour Osaloo, 2007). Research on the spore morphology of bryophytes has demonstrated that the structure and morphological characteristics of the sporoderm layer provide valuable insights into evolutionary processes, playing a crucial role in delineating both biological and taxonomic boundaries (Carrión et al., 1995; Brubaker et al., 1998; Estébanez, 2006; Khoshravesh and Osaloo, 2007; Medina et al., 2009; Schuette and Renzaglia, 2010; Brown et al., 2015; Piñeiro, 2017; Potoğlu Erkara et al., 2018; Luizi-Ponzo and Silva-e-Costa, 2019). Moreover, spore morphology is a critical factor in the species identification of thallose liverworts (Marchantiophyta). In fact, it serves as the sole systematic characteristic employed in the taxonomic identification of species within the genus *Fossombronia* Raddi. (Baros et al., 1993).

From the past to the present, many studies have shown the importance of spore morphology in taxonomy (McClymont, 1955; Boros and Járai-Komlódi, 1975; Mogensen, 1981; Blackmore and Barnes, 1991; Carrión et al., 1993; Luizi-Ponzo and Barth, 1999; Potoğlu Erkara, 2017; Silva-e-Costa and Luizi-Ponzo, 2019). However, the majority of bryophyte studies in Türkiye focus on floristic and ecological aspects, with research on spore morphology remaining relatively limited, though it is gradually increasing (Potoğlu Erkara and Savaroğlu, 2007; Savaroğlu et al., 2007; Savaroğlu and Potoğlu Erkara, 2008; Aşçı et al., 2010; Ceter et al., 2018; Gözcü et al., 2018a, 2018b; Aslan et al., 2022). In the present study, the spores of acrocarpous moss *Crossidium squamiferum* var. *pottioideum* (De Not.) Mönk. and pleurocarpous moss *Brachythecium salebrosum* (Hoffm. ex F. Weber & D. Mohr) Schimp. were investigated comparatively.

2. Material and Methods

The materials of the studied taxa were obtained from the special collection of Prof. Dr. Tülay EZER and the taxa are given in Figure 1 and detailed information about the taxa are given in Table 1.

The spore slides of the taxa, prepared using the Wodehouse (W) method (Wodehouse, 1935) and the acetolysis (A) method (Erdtman, 1960), were examined through light microscopy, and microphotographs of the spores were subsequently captured. Palynological investigations were performed using an Olympus CX31 light microscope equipped with an apochromatic oil immersion objective (100x) and micrometric periplane eyepieces (10x). Microphotographs were captured using an Olympus DP25 imaging system connected to this light microscope.

Given that the aperture of the spores is positioned at the proximal pole, measurements of the polar axis and equatorial axis were taken from the equatorial view. In the polar view, both the short and long equatorial diameters were recorded. Thus, the polar and equatorial axes were measured in the equatorial view, while the smallest and largest equatorial diameters were assessed in the polar view. In addition, measurements of the sporoderm layers (sclerine, intine) were measured 45 times until a Gaussian curve was obtained. The statistical values of the measurements (mean (M), standard deviation (S) and variations (Var.)) were evaluated with SPSS Statistics Vol. 22 prepared according to Sokal and Rohlf (1969).

In addition, detailed examinations of the spores by scanning electron microscope (SEM) were carried out at the Central Research Laboratory of Niğde Ömer Halisdemir University.

Figure 1. Habitus of the taxa (dry). a. *Brachythecium salebrosum*, b. *Crossidium squamiferum* var. *pottioideum*.

Table 1. Taxa and locality details. C.N.: Collection number.

Taxa	Locality	Date	C.N
Brachythecium salebrosum	Mersin, Anamur, Ermenek-Abanoz road, steppe,1450 m, 36º23'17.84"N 32º55'19.21"E.	22.09.2018	TE6146a
Crossidium squamiferum var. *pottioideum*	Mersin, Bozyazı, north of Kömürler neighbourhood, *Pinus brutia* forest, 700 m, 36º10'13.42"N 32º57'23.44"E.	29.01.2019	TP6349a

3. Findings

Equatorial and polar views of the spores of pleurocarpous *B. salebrosum* and acrocarpous *C. squamiferum* var. *pottioideum* were examined by light microscopy and scanning electron microscopy (SEM). The terminology of Erdtman (1969), Faegri and Iversen (1975) and Punt et al. (2007) were used to describe the spore morphology.

Table 2. Morphological measurements of the spores in their equatorial views. W: Wodehouse method, A: Acetolysis method, P: Polar axis, E: Equatorial axis, M: Mean, S: Standard deviation, Var.: Variation.

Taxa	Spore shape	P/E	Polar Axis (µm)			Equatorial Axis (µm)		
			M	S	Var.	M	S	Var.
B. salebrosum (A)	Suboblat	0.83	7.60	±1.35	6.00-11.00	12.08	±1.18	9.00-15.00
B. salebrosum (W)	Oblat	0.73	10.13	±1.70	7.00-15.00	12.26	±1.64	10.00-18.00
C. squamiferum var. *pottioideum* (A)	Oblat	0.64	6.75	±0.93	5.00-9.00	10.11	±1.66	8.00-14.00
C. squamiferum var. *pottioideum* (W)	Oblat	0.68	7.57	±1.40	5.00-11.00	10.60	±1.42	8.00-16.00

Table 3. Morphological measurements of the spores in their polar views. W: Wodehouse method, A: Acetolysis method, D_m: The shortest equatorial diameter, D_M: The largest equatorial diameter, M: Mean, S: Standard deviation, Var.: Variation.

Taxa	**D_m (µm)**			**D_M (µm)**		
	M	**S**	**Var.**	**M**	**S**	**Var.**
B. salebrosum (A)	9.86	±0.89	8.00-12.00	10.73	±0.96	9.00-13.00
B. salebrosum (W)	11.86	±2.15	9.00-20.00	13.22	±2.48	10.00-25.00
C. squamiferum var. *pottioideum* (A)	8.33	±1.49	6.00-13.00	10.28	±1.61	8.00-14.00
C. squamiferum var. *pottioideum* (W)	9.15	±1.12	7.00-11.00	10.26	±1.26	8.00-15.00

Table 4. Morphological observations and measurements of the sporoderm layers of the spores. W: Wodehouse method, A: Acetolysis method.

Taxa	**Sclerine (µm)**	**Intine (µm)**	**Aperture type**	**Ornamentation**
B. salebrosum (A)	0.70 (±0.10)	-	Monolete, Trilete	Gemmate
B. salebrosum (W)	0.74 (±0.06)	0.50 (±0.03)	Monolete, Trilete	Gemmate
C. squamiferum var. *pottioideum* (A)	0.56 (±0.12)	-	Monolete, Trilete	Verrucate
C. squamiferum var. *pottioideum* (W)	0.78 (±0.08)	0.53 (±0.08)	Monolete, Trilete	Verrucate

3.1. Descriptions of the spores

***Brachythecium salebrosum*:** As a result of the morphological measurements made on the preparations prepared by the Wodehouse method, the polar axis length of the spores belonging to the taxon is 10.12 µm on average and the equatorial axis length is 12.26 µm on average. Given that the ratio of the polar axis length to the equatorial axis length of the spores was 0.73 µm, the spores were classified as oblate in shape. Due to the inability to distinctly separate the exine and perine layers of the spores under the light microscope, measurements were taken of the sclerine layer. The sclerine has an average thickness of 0.74 µm and the intine has an average thickness of 0.50 µm and the aperture type is monolette (Table 2, Fig. 2).

On the other hand, as a result of the morphological measurements made on the preparations prepared by acetolysis method, the polar axis length of the spores belonging to the taxon is 7.6 µm, while the equatorial axis length is 12.08 µm. The ratio of the polar to the equatorial axis length of the spores is 0.83 µm, indicating that the spores were classified as suboblate in shape. Due to the inability to distinctly separate the exine and perine layers of the spores under the light microscope, the sclerine layer was measured and determined to have an average thickness of 0.70 µm. Aperture type is monolete. Ornamentation type is gemmate (Table 2, Figs. 2,3).

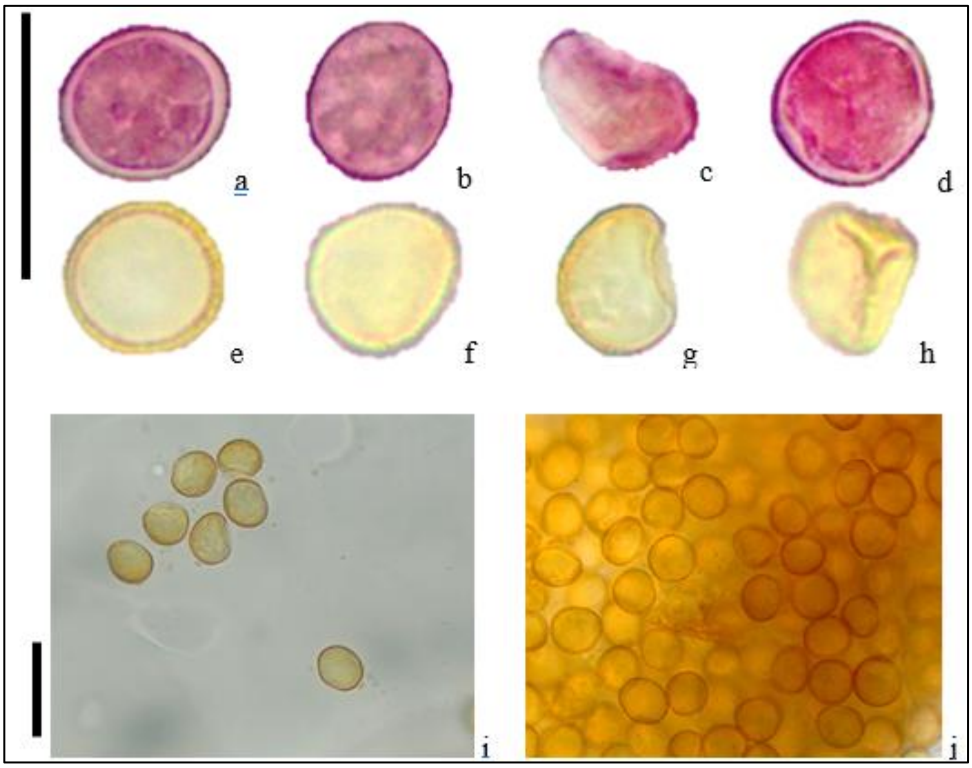

Figure 2. Microphotograps of *B. salebrosum* spores (LM). a: Optical section (W), b: Equatorial view, ornamentation (W), c: Equatorial view of monolete spore (W), d: Proximal pole of trilete spore (W), e: Optical section (A), f: Equatorial view, ornamentation (A), g: Equatorial view of monolete spore (A), h: Proximal pole of trilete spore (A), i-j: Different appearances of spores (A) (Scale bars: 20 µm).

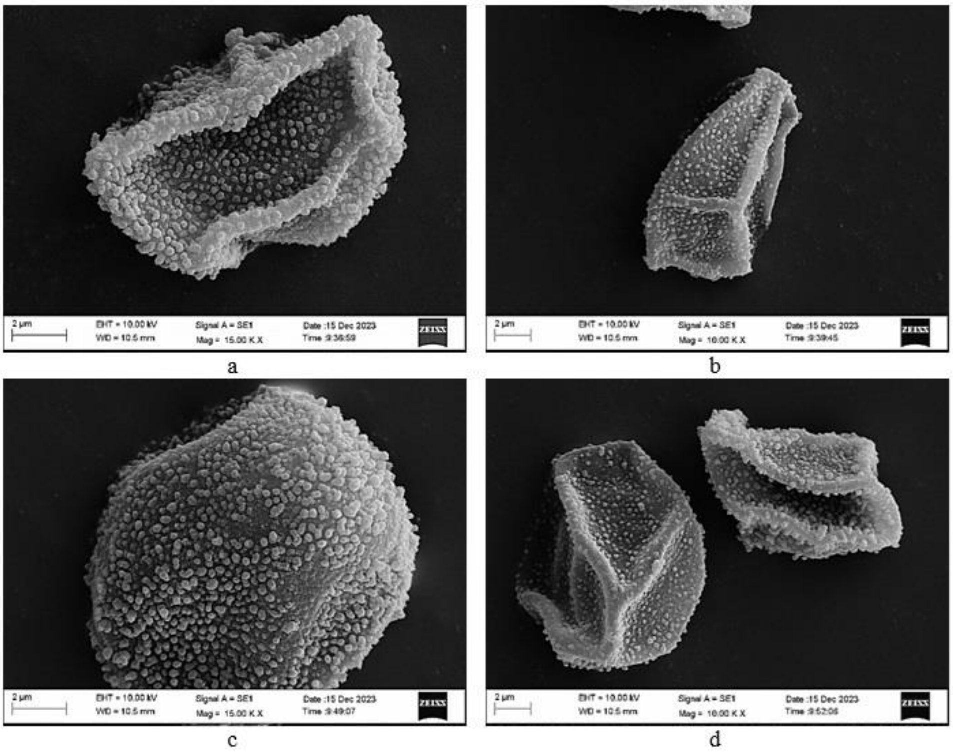

Figure 3. Microphotograps of *B. salebrosum* spores (SEM). a: Proximal pole of monolete spore, b: Proximal pole of trilete spore, c: Ornamentation, d: Different appearances of spores.

***Crossidium squamiferum* var. *pottioideum*:** As a result of the morphological measurements made on the preparations prepared by the Wodehouse method, the polar axis length of the spores belonging to the taxon is 7.57 µm on average and the equatorial axis length is 10.60 µm on average. Since the ratio of the polar axis length to the equatorial axis length of the spores was 0.68 µm, the spores were classified as oblate in shape. Due to the inability to distinctly separate the exine and perine layers of the spores under the light microscope, measurements were taken of the sclerine layer. The sclerine is 0.78 µm thick and the intine is 0.53 µm thick. The aperture type was observed to be monolete and trilete (Table 2, Fig. 4).

On the other hand, as a result of the morphological measurements made on the preparations prepared by acetolysis method, the polar axis length of the spores belonging to the taxon is 6.75 µm on average and the equatorial axis length is 10.11 µm on average. Since the ratio of the polar axis length to the equatorial axis length of the spores was 0.64 µm, the spores were classified as oblate in shape. Since the separation of the exine and perine layers of the spores could not be clearly separated in the light microscope, the sclerine layer was measured. The sclerine is 0.56 µm. Aperture type is monolete and trilete. Ornamentation type is verrucate (Table 2, Figs. 4,5).

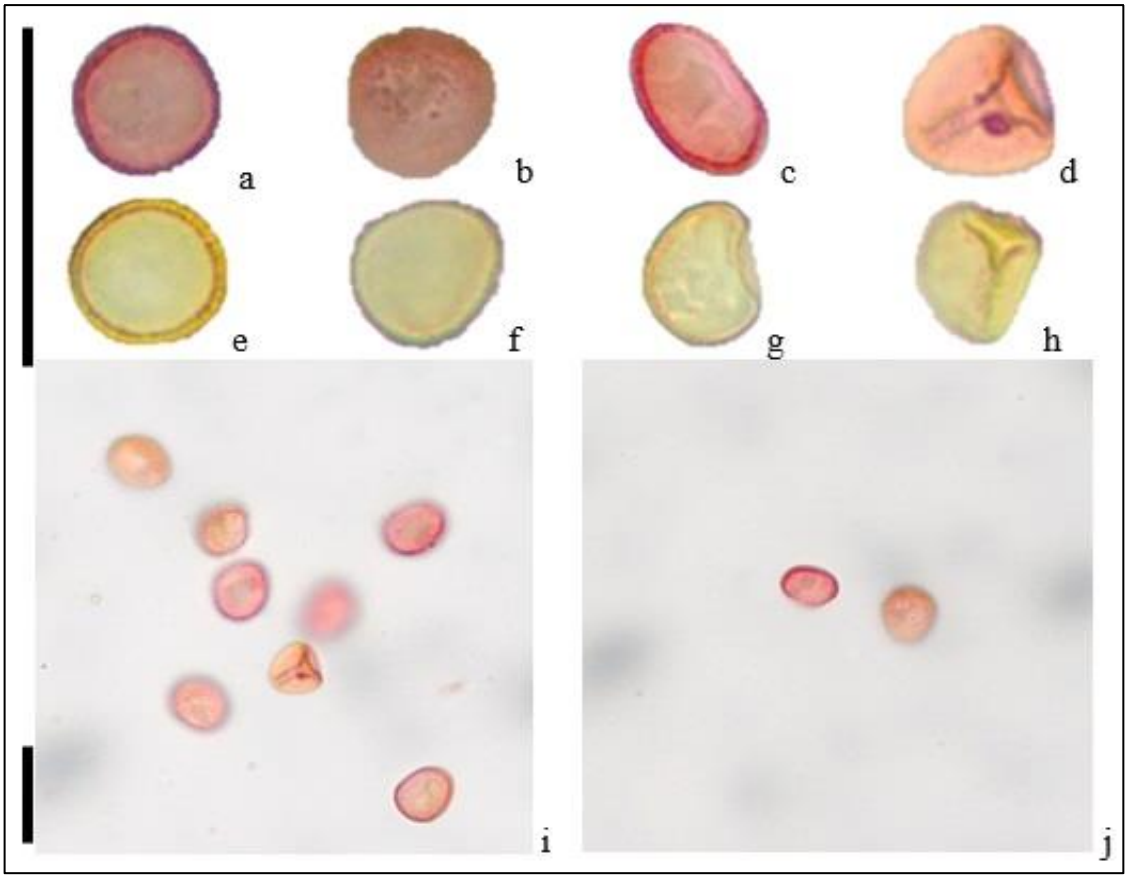

Figure 4. Microphotograps of *C. squamiferum* var. *pottioideum* spores (LM). a: Optical section (W), b: Ornamentation (W), c: Equatorial view of monolete spore (W), d: Proximal pole of trilete spore (W), e: Optical section (A), f: Equatorial view, ornamentation (A), g: Equatorial view of monolete spore (A), h: Proximal pole of trilete spore (A), i-j: Different appearances of spores (W) (Scale bars: 20 µm).

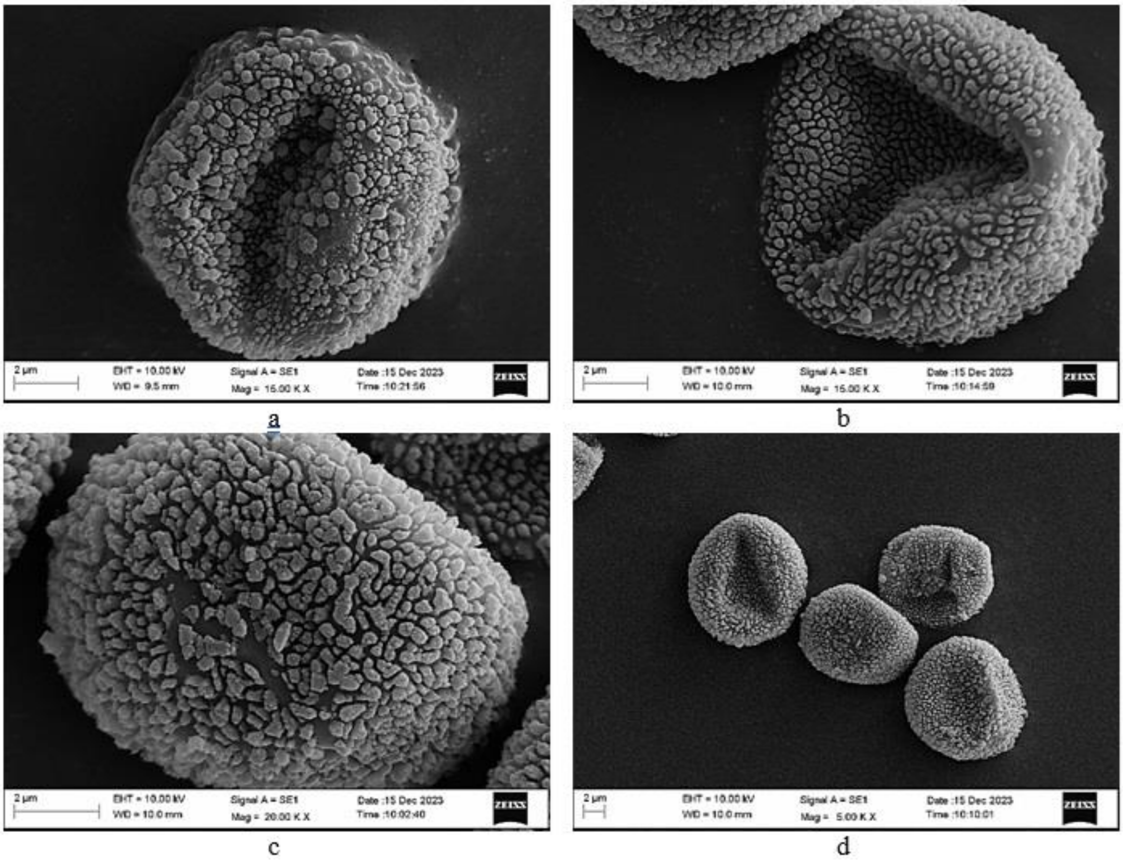

Figure 5. Microphotograps of *C. squamiferum* var. *pottioideum* spores (SEM). a: Proximal pole of monolete spore, b: Proximal pole of trilete spore, c: Ornamentation, d: Different appearances of spores.

4. Results and Discussion

Especially for taxa that are difficult to diagnose and identify taxonomically, palynological studies can be very important guides (Costa Silva-e-Costa and Luizi-Ponzo, 2019). Taxonomic analyses frequently incorporate data from palynological surveys on bryophyte spores, which offer a deeper insight into the taxonomy and ecology of the species (Carrión et al., 1995; Passarella and Luizi-Ponzo, 2019; Shumilovskikh et al., 2021; Gonçalves-Esteves et al., 2022). The morphological description of bryophyte spores is significant from a taxonomic and evolutionary standpoint, and it aligns with the species' biology, ecology, and habitat traits (Luizi-Panzo and Melhem, 2006).

Investigating the morphological traits of spores in bryophytes holds significant importance from both taxonomic and evolutionary standpoints, aligning closely with the biology of the species as well as its ecological and habitat characteristics (Luizi-Panzo and Melhem, 2006). In the present study, the spore morphologies of acrocarpous moss *C. squamiferum* var. *pottioideum* and pleurocarpous moss *B. salebrosum* were investigated. The spores of *C. squamiferum* var. *pottioideum*, which is distributed in arid habitats, vary between 6-10 µm. On the other hand, the spores of *B. salebrosum*, which prefers more humid habitats, vary between 7-13 µm and have relatively larger spores. Small particles are dispersed further than large particles due to lower settling velocities and expected longer air residence times (Hall and Walter, 2011; Zanatta et al., 2016). Moss spores are usually quite small (mostly <50 µm) and are therefore likely to be easily transported long distances by wind when they reach higher air masses, resulting in species with small spores being spread over larger areas (Johansson et al., 2014). Additionally, the relationship between spore collapse rate and spore diameter was experimentally supported (Aylor, 2002; Hussein et al., 2013). Compared to pleurocarpic *B. salebrosum*, the smaller spores of acrocarpic *C. squamiferum* var. *pottioideum*, which is distributed in arid habitats, may result in both more spores in the capsule and relatively longer distances of dispersal from the capsule. Thus, the probability of generation continuity is increased. On the other hand, while the relatively larger size of the spores of the pleurocarpic *B. salebrosum* may limit the species' dispersal potential, these single-celled spores, characterized by their chloroplasts and abundant protoplasm, possess the ability to survive until the requisite water and moisture conditions for germination are met.

In conclusion, palynological investigations into bryophyte spores will significantly contribute to make significant contributions to both their taxonomic classification and the understanding of the ecological complexities inherent in these ancient plants throughout history. It will also provide a source of data for further taxonomic, palaeobotanical and ecological studies.

Declaration

Acknowledgments
This study was financially supported by the Scientific and Technological Research Council of Turkey (TÜBİTAK) within the scope of 2209-A - Research Project Support Programme for Undergraduate Students (Application Number: 1919B012223572).

Author contributions
Idea/Concept: ZAE, TE; Conceptualization and design: ZAE, TE, EA; Auditing consulting: ZAE, TE; References: ZAE, EA, TE; Materials: ZAE, TE, EA; Data collection and/or processing: ZAE, EA; Analysis and/or interpretation: ZAE, EA, TE; Literature search: ZAE, EA; Writing phase: ZAE, EA, TE; Critical review: ZAE, TE.

Conflict of interest
The authors have no competing interests to declare in relation to the content of this article.

Funding
This study was financially supported by the Scientific and Technological Research Council of Turkey (TÜBİTAK) within the scope of 2209-A - Research Project Support Programme for Undergraduate Students (Application Number: 1919B012223572).

Ethical approval
This research does not involve human or animal subjects and therefore does not require ethical approval.

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