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

DOI: 10.26672/anatolianbryology.1189719

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

Spore Morphologies of Some Acrocarpous Mosses (Bryophyta): Taxonomical and Ecological Significance

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Received: 15 October 2022 **Revised: 31 October 2022** **Accepted: 4 November 2022**

Abstract

In this study, the spore morphologies of five different acrocarpous moss species (*Weissia brachycarpa*, *Distichium inclinatum*, *Pterygoneurum ovatum*, *Ceratodon purpureus* and *Ptychostomum donianum*) were investigated and discussed the taxonomical and ecological value of spores morphological characters of these species. Spores were prepared according to standard palynological techniques such as acetolysis and Wodehouse and analyzed using light microscopy to reveal sporoderm structures. The spores of the three moss species except *Pterygoneurum ovatum* and *Ceratodon purpureus* which are heteromorph are heteropolar and monolete. Also, in all species, the shape of the spores was determined as suboblate in equatorial view. In polar views, the shapes of spores vary as oblate-spheroid and suboblate. In equatorial view of the spores, the length of the polar axis (P) range from 9.60 µm to 27.90 µm on average, the length of the equatorial axis (E) is between 12.00 µm and 31.96 µm on average. The sporoderm layers of the spores were also examined and measured. It has been determined that the spores of the examined species have five different ornamentation types as verrucate, clavate-gemmate, baculate, clavate and baculate-clavate. The results obtained are discussed in terms of taxonomical and ecological aspects.

Keywords: Acrocarpous, Bryophyte, Moss, Spore, Taxonomy.

Bazı Akrokarp Karayosunlarının (Bryophyta) Spor Morfolojileri: Taksonomik ve Ekolojik Önemi

Öz

Bu çalışmada, beş farklı akrokarp karayosunu türünün (*Weissia brachycarpa*, *Distichium inclinatum*, *Pterygoneurum ovatum*, *Ceratodon purpureus* ve *Ptychostomum donianum*) spor morfolojileri araştırılmış ve bu türlerin palinolojik karakterlerinin taksonomik ve ekolojik önemi tartışılmıştır. Sporlar, asetoliz ve Wodehouse gibi standart palinolojik tekniklere göre hazırlanmış ve sporoderm yapılarını ortaya çıkarmak için ışık mikroskobu kullanılarak analiz edilmiştir. Heteromorf olan *Pterygoneurum ovatum* ve *Ceratodon purpureus* dışındaki üç karayosunu türünün sporları heteropolar ve monolettir. Ayrıca, tüm türlerde sporların şekli ekvatoral görünüşte suboblat olarak tespit edilmiştir. Polar görünüşlerde, sporların şekilleri oblate-sferoid ve suboblate olarak değişmektedir. Sporların ekvatoral görünüşte polar ekseninin uzunluğu (P) ortalama 9,60 µm ile 27,90 µm arasında, ekvator ekseninin (E) uzunluğu ise ortalama 12,00 µm ile 31,96 µm arasındadır. Sporların sporoderm tabakaları da incelenmiş ve ölçümleri yapılmıştır. İncelenen türlerin sporlarının verrukat, klavat-gemmat, bakulat, klavat ve bakulat-klavat olmak üzere beş farklı süsleme tipine sahip olduğu belirlenmiştir. Elde edilen sonuçlar taksonomik ve ekolojik açıdan tartışılmıştır.

Anahtar kelimeler: Akrokarp, Briyofit, Karayosunu, Spor, Taksonomi

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To cite this article: Aslan Z. Çulha H. Ezer T. Doğan C. *2022. Spore Morphologies of Some Acrocarpous Mosses (Bryophyta): Taxonomical and Ecological Significance. Anatolian Bryology. 8:2, 106-113.*

1. Introduction

Bryophytes, which form the second largest group of land plants, spread in various habitats of almost all continents from the equator to the polar regions and contain about 20.000 species (Glime, 2022). Since bryophytes, which can balance their internal water balance according to the external environment, that is, with poikilohydric characteristics, do not have a developed vascular system, they take the water and dissolved mineral substances necessary for survive from the environment by diffusion with their all surfaces. Therefore, they are very sensitive to the abiotic ecological factors of the habitat (Schofield, 2001; Crum, 2001). Generally distributed in habitats where water and moisture are limited, members of acrocarpous mosses show strong adaptations to drought (Smith, 2004).

Haploid (n) gametophyte and diploid (2n) sporophyte generation are seen in these plants which have haplodiplontic life cycle (Simpson, 2012). In addition to gametophytic and sporophytic characters, spore morphologies are of great importance in paleobotanical, taxonomic and ecological terms in these plants, which reproduce with small single-celled spores of 7 µm (some *Grimmia* species) to 250 µm (some *Archidium* species) (Khoshravesh and Kazempour Osaloo, 2007). Studies on spore morphologies of bryophytes have revealed that intin structure and morphological characterization are a potential source of data on evolutionary processes in determining both biological and taxonomic boundaries (Carrion et al., 1995; Estébanez, 2006; Khoshravesh and Osaloo, 2007; Medina et al., 2009; Savaroğlu, 2015; Potoğlu Erkara et al., 2018). This situation plays an important role in the species identification of thallus liverworts (Marchantiophyta), especially *Fossombronia* Raddi. Spore morphology is the only distinctive systematic character in the diagnosis of *Fossombronia* members (Baros et al., 1993).

Although spore morphology in bryophytes has a limited value in taxonomy, studies on this subject are increasing rapidly and spore characteristics are widely used in bryophyte taxonomy and identification of new species. However, the majority of the studies on bryophytes in Türkiye are floristic and ecological, and the studies on spore morphologies are very limited (Potoğlu Erkara and Savaroğlu, 2007; Savaroğlu et al., 2007; Savaroğlu and Potoğlu Erkara, 2008; Aşçı et al., 2010; Savaroğlu, 2015; Çeter and Canlı, 2016; Çeter et al., 2018; Gözcü et al., 2018a, 2018b). In this study, spore morphologies of five different moss (Bryophyta) species (*Weissia brachycarpa* (Nees & Hornsch.) Jur., *Distichium inclinatum* (Hedw.) Bruch & Schimp., *Pterygoneurum ovatum* (Hedw.) Dixon, *Ceratodon purpureus* (Hedw.) Brid. and, *Ptychostomum donianum* (Grev.) Holyoak & N. Pedersen) were investigated and it was aimed to provide complementary palynological data as well as taxonomic and ecological characteristics of these species.

2. Material and Methods

The bryophyte specimens, which are the study material in this study, were provided by Prof. Dr. Tülay EZER's special bryophyte collection and the data of the localities where the specimens were collected are given in Table 1. Spore slides of each species prepared according to the Wodehouse (W) (Wodehouse, 1935) and acetolysis methods (A) (Erdtman, 1960) were examined with a light microscope and their microphotographs were taken.

Palynological examinations were made with an Olympus CX31 light microscope, and apochromatic oil immersion objective (100x) and micrometric periplane eyepiece (10x) were used during the examinations. Microphotographs were taken with the Olympus E-330 camera system connected to a light microscope.

Polar axis and equatorial axis were measured in the equatorial view, while the short equatorial diameter and the large equatorial diameter were measured in the polar view. In addition, the sclerine, perine, exine, sexine and nexine measurements of spores in polar and equatorial views were measured at least 30 times and at most 50 times until the Gaussian curve was obtained. The mean (M), standard deviation (S) and variations (Var.) of the measurements made were evaluated in the SPSS Statistics 22 software prepared according to Sokal and Rohlf (1969).

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

Species	Locality	Date	C.N
Ceratodon purpureus	Adana, Pozantı, Karınca Mountain, Karabeydere place, on soil, 1250m., 37°32'6.70"N-34°52'18.53"E	15.06.2020	T.E.2155
Distichium inclinatum	Niğde, Aladağlar National Park, Narpuz Valley, on soil, 2600m., 37°49'330"N-35°08'190"E	16.10.2011	T.E.2132
Pterygoneurum ovatum	Niğde, Niğde Ömer Halisdemir University, Campus area, behind the Faculty of Science, on soil, 1200m., 37°56'31.00"N, 34°37'38.00"E	19.05.2022	T.E.2853
Ptychostomum donianum	Adana, Pozantı, Karınca Mountain, Kurtderesi place, on soil, 1500m., 37°30'53.55"N-34°52'55.32"E	09.03.2021	T.E.2314
Weissia brachycarpa	Mersin, Bozyazı, Evciler Village, on soil, 100m., 36° 9'10.80"N, 32°54'0.61"E	22.03.2019	T.E.2183

3. Results

The equatorial (Table 2) and polar views (Table 3) of spores of acrocarpous mosses species *Weissia brachycarpa*, *Distichium inclinatum*, *Pterygoneurum ovatum*, *Ceratodon purpureus* and *Ptychostomum donianum* were examined and described under the light microscope. Terminologies of Erdtman (1969), Faegri and Iversen (1975), Boros and Járai-Komlódi (1975), Blackmore and Barnes (1991), Punt et al. (2007) and Kapp et al. (2000) were used to description of the spore morphologies. The morphological measurements of the sporoderm layers of the spores were determined by examining the spore preparations prepared by the acetolysis method and are given in Table 4.

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

Species	Spore shape	P/E	Polar Axis (µm)			Equatorial Axis (µm)		
			M	S	Var.	M	S	Var.
Ceratodon purpureus (A)	Suboblate	0.85	10.33	±1.18	7.00-12.00	12.17	±0.83	11.00-14.00
Ceratodon purpureus (W)	Suboblate	0.80	9.60	±1.16	7.00-11.00	12.00	±1.08	10.00-14.00
Distichium inclinatum (A)	Suboblate	0.83	24.30	±1.90	21.00-28.00	29.23	±1.63	27.00-32.00
Distichium inclinatum (W)	Suboblate	0.82	23.07	±1.53	20.00-26.00	28.17	±1.56	25.00-31.00
Pterygoneurum ovatum (A)	Suboblate	0.87	27.90	±2.98	22.00-35.00	31.96	±2.10	27.00-37.00
Pterygoneurum ovatum (W)	Suboblate	0.79	19.00	±1.53	15.00-20.00	24.13	±1.46	21.00-27.00
Ptychostomum donianum (A)	Suboblate	0.83	10.00	±0.69	9.00-11.00	12.07	±0.78	10.00-13.00
Ptychostomum donianum (W)	Suboblate	0.86	11.07	±0.64	10.00-12.00	12.80	±0.85	11.00-14.00
Weissia brachycarpa (A)	Suboblate	0.80	14.57	±1.48	13.00-18.00	18.23	±0.73	16.00-19.00
Weissia brachycarpa (W)	Suboblate	0.82	14.63	±1.00	13.00-17.00	17.83	±0.70	17.00-19.00

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

Species	Spore shape	D_m (µm)			D_M (µm)		
		M	S	Var.	M	S	Var.
Ceratodon purpureus (A)	Oblate-spheroid	10.93	±0.94	9.00-13.00	12.27	±0.91	10.00-14.00
Ceratodon purpureus (W)	Suboblate	9.90	±1.06	7.00-12.00	11.70	±1.09	10.00-13.00
Distichium inclinatum (A)	Oblate-spheroid	26.03	±1.65	23.00-30.00	28.53	±1.22	26.00-32.00
Distichium inclinatum (W)	Oblate-spheroid	25.70	±1.56	23.00-30.00	28.00	±1.55	26.00-32.00
Pterygoneurum ovatum (A)	Suboblate	28.60	±2.11	24.00-34.00	33.23	±1.50	31.00-36.00
Pterygoneurum ovatum (W)	Suboblate	20.67	±1.99	17.00-25.00	24.43	±2.58	20.00-29.00
Ptychostomum donianum (A)	Suboblate	10.53	±0.94	9.00-12.00	12.07	±0.98	10.00-14.00
Ptychostomum donianum (W)	Oblate-spheroid	11.63	±0.67	11.00-13.00	12.80	±0.61	12.00-14.00
Weissia brachycarpa (A)	Oblate-spheroid	17.13	±0.78	15.00-19.00	18.43	±1.04	17.00-21.00
Weissia brachycarpa (W)	Oblate-spheroid	16.77	±0.68	15.00-18.00	18.00	±0.53	17.00-19.00

Table 4. Morphological observations and measurements of sporoderm layers of the spores.

Species	Sclerine (µm)	Perine (µm)	Exine (µm)	Sexine (µm)	Nexine (µm)	Aperture type	Ornamentation
Ceratodon purpureus	-	0.62 (±0.22)	0.90 (±0.20)	-	-	Monolete, Trilete	Verrucate
Distichium inclinatum	1.13 (±0.22)	-	-	-	-	Monolete	Clavate-Gemmate
Pterygoneurum ovatum	-	0.75 (±0.25)	0.97 (±0.13)	-	-	Monolete, Trilete	Baculate
Ptychostomum donianum	-	0.44 (±0.09)	0.92 (±0.19)	-	-	Monolete	Clavate
Weissia brachycarpa	-	0.73 (±0.23)	1.00 (±0.00)	0.50 (±0.00)	0.50 (±0.00)	Monolete	Baculate-Clavate

3.1. Descriptions of the spores:

***Ceratodon purpureus*; **spores are heteropolar and heteromorph. When the slides were examined, trilete spores were also detected at the rate of 15.82 % besides that monolete spores. The spore shape is suboblate (P/E 0.85 (A), 0.80 (W)) in equatorial view, oblate-spheroid (A) and suboblate (W) in polar view (Table 2,3). In the equatorial view, the polar axis length is 10.33 µm (A), 9.60 µm (W) on average while, the equatorial axis length is 12.17 µm (A), 12.00 µm (W) on average (Table 2). In the polar view, the short equatorial diameter is 10.93 µm (A), 9.90 µm (W) on average and the large equatorial diameter is 12.27 µm (A), 11.70 µm (W) on average (Table 3). Since the separation of perine and exine layers can be observed in spores of the species, the measurement of the sclerine was not performed. On the other hand, since the separation of the sexine and nexine layers could not be observed clearly, the thickness of these layers could not be measured. The perine is 0.62 µm on average and the exine is 0.90 µm on average (Table 4). The spore surface ornamentation is verrucate (Fig. 1). The boundaries of the concave leptoma at proximal pole are irregular.

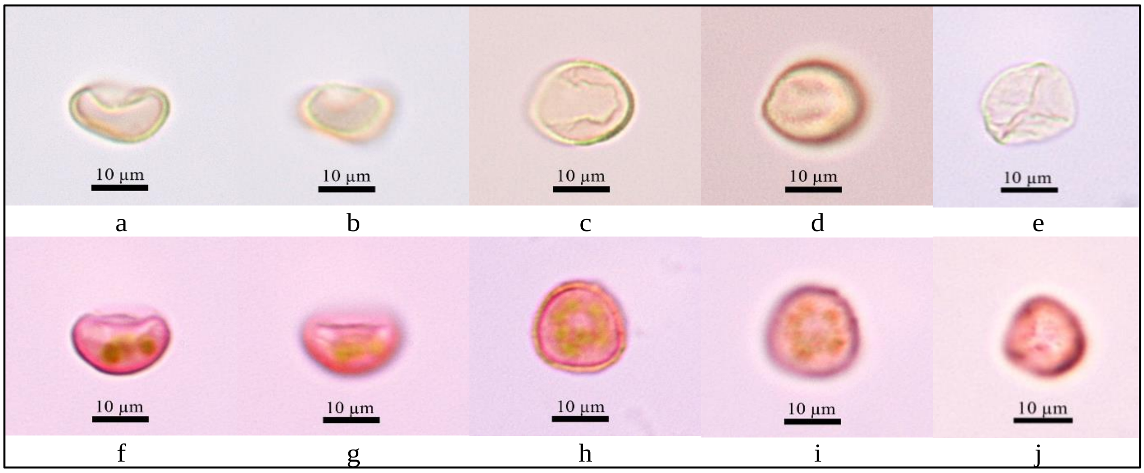

Figure 1. Microphotograps of *Ceratodon purpureus* spores. a: Optical section of equatorial view (A), b: Equatorial view, ornamentation (A), c: Proximal pole of monolete spore (A), d: Polar view, ornamentation (A), e: Proximal pole of trilete spore (A), f: Optical section of equatorial view (W), g: Equatorial view, ornamentation (W), h: Optical section of proximal pole of monolete (W), i: Distal pole, ornamentation (W), j: Proximal pole of trilete spore (W).

***Distichium inclinatum*; **spores are heteropolar and monolete. In equatorial view, P/E 0.83 (A), 0.82 (W), the spore shape is suboblate, in polar view oblate-spheroid (A) (W) (Table 2,3). In the equatorial view, the polar axis length is 24.30 µm (A), 23.07 µm (W) on average and the equatorial axis length is 29.23 µm (A), 28.17 µm (W) on average (Table 2). In the polar view, the short equatorial diameter is 26.03 µm (A), 25.70 µm (W) on average while, the large equatorial diameter is 28.53 µm (A), 28.00 µm (W) on average (Table 3). Since the separation of perine and exine layers could not be clearly observed in spores belonging to the species, the sclerine were measured. As a result of the examinations, it was determined that the sclerine was 1.13 µm thick on average (Table 4). The spore surface ornamentation is clavate-gemmate (Fig. 2). The borders of the concave leptoma, which forms the aperture region in spores, are irregular and indistinct (Fig. 2a-d).

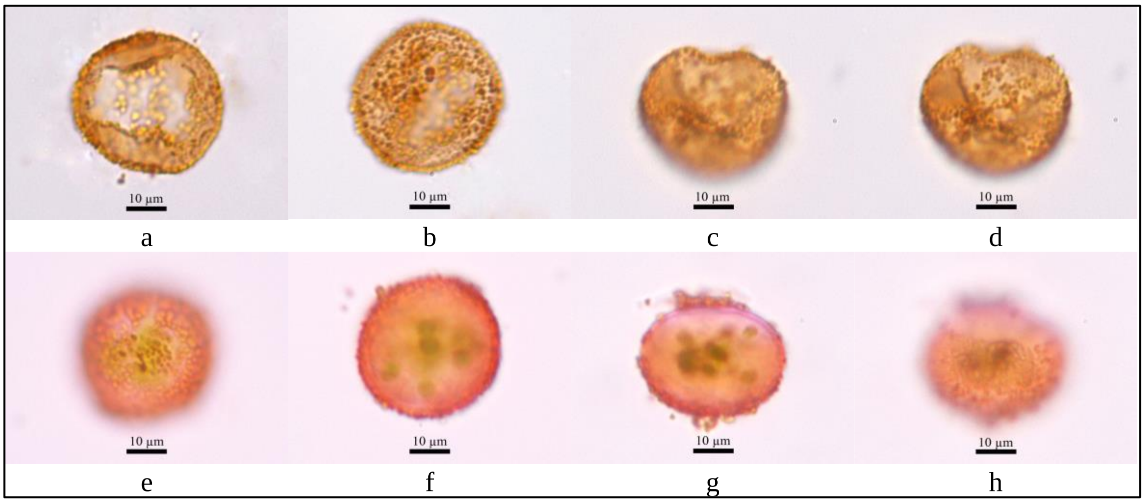

Figure 2. Microphotograps of *Distichium inclinatum* spores. a: Proximal pole, leptoma (A), b: Distal pole, ornamentation (A), c: Optical section of equatorial view (A), d: Equatorial view, ornamentation (A), e: Distal pole, ornamentation (W), f: Optical section of polar view (W), g: Optical section of equatorial view (W), h: Equatorial view, ornamentation (W).

***Pterygoneurum ovatum*;** spores are heteropolar. While the spores are mostly monolet, 33.28% of spores is trilete. Therefore, the species has heteromorph spores. In equatorial view (P/E 0.87 (A), 0.79 (W)) and in polar view, the spore shape is suboblate (A) (W) (Table 2,3). In the equatorial view, the polar axis length is 27.90 µm (A), 19.00 µm (W) on average while, the equatorial axis length is 31.96 µm (A), 24.13 µm (W) on average (Table 2). In the polar view, the short equatorial diameter is 28.60 µm (A), 20.67 µm (W) on average and the large equatorial diameter is 33.23 µm (A), 24.43 µm (W) on average (Table 3). The measurement of the sclerine was not performed because of the separation of perine and exine layers can be observed in spores of the species. On the other hand, since the separation of the sexine and nexine layers could not be observed clearly, the thickness of these layers could not be measured. The very prominent perine is 0.75 µm on average, and the exine is 0.97 µm on average (Table 4). The spore surface ornamentation is baculate (Fig. 3). Concave leptoma borders are distinct, but vary in width.

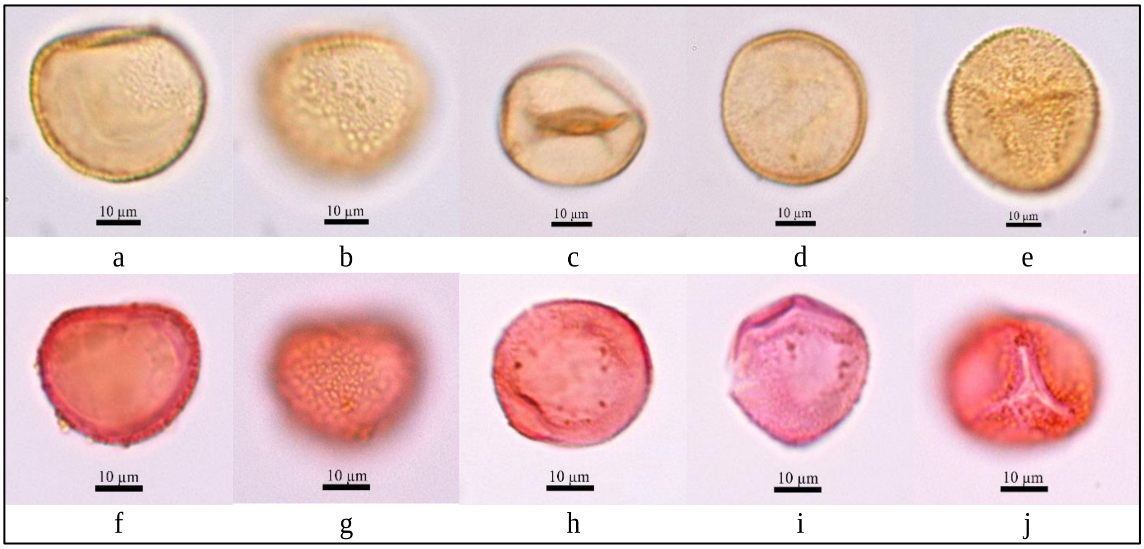

Figure 3. Microphotograps of *Pterygoneurum ovatum* spores. a: Optical section of equatorial view (A), b: Equatorial view, ornamentation (A), c: Proximal pole of monolete spore (A), d: Optical section of monolete spore in polar view (A), e: Distal pole of trilete spore (A), f: Optical section of equatorial view (W), g: Equatorial view, ornamentation (W), h: Proximal pole of monolete spore (W), i: Equatorial view of trilete spore (W), j: Proximal pole of trilete spore (W).

***Ptychostomum donianum*;** spores are heteropolar and monolete. The spore shape is suboblate (P/E 0.83 (A), 0.86 (W)) in equatorial view, suboblate (A) and oblate-spheroid (W) in polar view (Table 2,3). In the equatorial view, the polar axis length is 10.00 µm (A), 11.07 µm (W) on average and the equatorial axis length is 12.07 µm (A), 12.80 µm (W) on average (Table 2). In the polar view, the short equatorial diameter 10.53 µm (A), 11.63 µm (W) on average while, the large equatorial diameter is 12.07 µm (A), 12.80 µm (W) on average (Table 3). Since the perine and exine can be measured separately in spores of the species, the measurement of the sclerine was not performed. On the other hand, since the separation of the sexine and nexine layers could not be clearly observed, the thickness of these layers could not be measured. The perine is 0.44 µm on average and the exine is 0.92 µm on average (Table 4). The spore surface ornamentation is clavate (Fig. 4). The borders of the concave leptoma are distinct and varies between 2-6 µm in width (Fig. 4a-c).

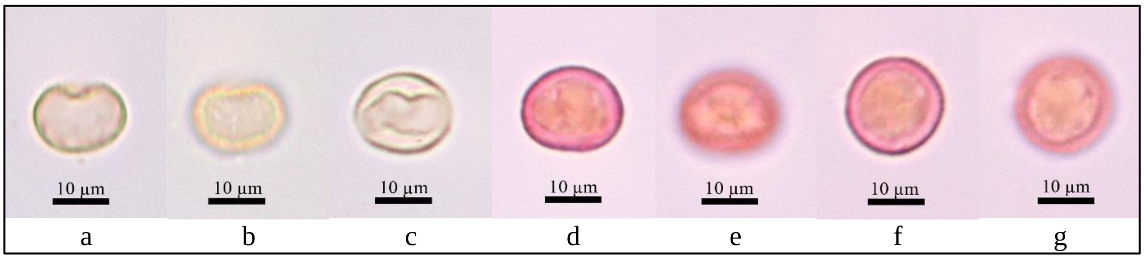

Figure 4. Microphotograps of *Ptychostomum donianum* spores. a.: Optical section of equatorial view (A) b: Equatorial view, ornamentation (A), c: Proximal pole, leptoma (A), d: Optical section of equatorial view (W), e: Equatorial view, ornamentation (W), f: Optical section of polar view (W), g: Distal pole, ornamentation (W).

***Weissia brachycarpa*;** spores are heteropolar and monolete. In equatorial view, P/E 0.80 (A), 0.82 (W), spore shape is suboblate (A), (W). In polar view, spore shape is oblate-spheroid (A), (W) (Table 2,3). In the equatorial view, the polar axis length is 14.57 µm (A), 14.63 µm (W) on average and the equatorial axis length is 18.23 µm (A), 17.83 µm (W) (Table 2). In the polar view, the short equatorial diameter is 17.13 µm (A), 16.77 µm (W) on average while, the large equatorial diameter is 18.43 µm (A), 18.00 µm (W) (Table 3). The separation of perine and exine layers could be clearly observed in spores belonging to the species. Therefore, the measurement of the sclerine was not performed. The perine, which is quite prominent, is 0.73 µm on average, the exine is 1.00 µm on average, and the sexine and nexine are 0.50 µm thick (Table 4). The spore surface ornamentation is baculate-clavate (Fig. 5). Also, the spores of the *W. brachycarpa* have concave leptoma (Fig. 5a,b,e).

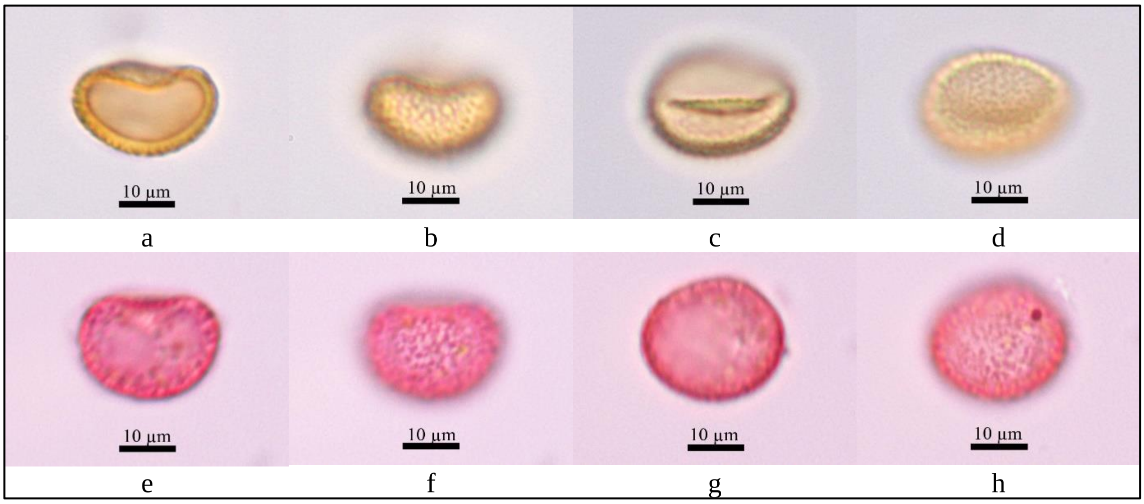

Figure 5. Microphotograps of *Weissia brachycarpa* spores. a.: Optical section of equatorial view (A), b: Equatorial view, ornamentation (A), c: Proximal pole, leptoma (A), d: Distal pole, ornamentation (A), e: Optical section of equatorial view (W), f: Equatorial view, ornamentation (W), g: Optical section of polar view (W), h: Distal pole, ornamentation (W).

4. Discussion

Palynological studies can provide very important guiding contributions especially for taxa that have difficulties in diagnosis and identification in terms of taxonomy (Costa Silva-e-Costa and Luizi-Ponzo, 2019). Data from palynological studies on bryophyte spores lead to a better understanding of the taxonomy and ecology of species and are widely used in taxonomic analyzes such as identification and descriptions of these species (Carrion et al., 1995; Can Gözcü et al., 2018). The morphological characterization of spores in bryophytes is important both taxonomically and evolutionarily and is compatible with the biology, ecological and habitat characteristics of the species (Luizi-Panzo and Melhem, 2006). In the present paper, spore morphologies of acrocarpous moss species *Weissia brachycarpa*, *Distichium inclinatum*, *Pterygoneurum ovatum*, *Ceratodon purpureus* and *Ptychostomum donianum* were studied using light microscopy. Among them, the spores of *W. brachycarpa* have previously been observed by Can Gözcü et. al. (2018). It was determined that the spore morphology results of the species were relatively compatible with this study. In the present study, the spores of the *W. brachycarpa* are heteropolar and spore shape is oblate-spheroid (A), (W). Acrocarpous mosses include members that grow perpendicular to their substrate and often show strong adaptations to drought (Goffinet and Shaw, 2009). It was determined that the spores of the all species were small size in the present study (Table 2,3). This can be thought of as an adaptability against the drought stress that the spores of bryophytes, the ancestors of living land plants, will encounter when they are dispersed from the capsule. At the same time, these small-sized, chloroplast-bearing and abundant protoplasm single-celled spores increase the spreading potential of the species and will have the ability to survive until they provide the water and moisture conditions necessary for their germination.

While it was observed that the *D. inclinatum*, *P. donianum* and *W. brachycarpa* had homogeneous spores with only monelete aperture, it was determined that *C. purpureus* and *P. ovatum* had both monolete and trilete spores, that is, they were heteromoph spores (Figs. 1-5, Table 4). Thus, it can be said that the heteromorphous spores of these two species may increase the germination chance of their spores compared to other species.

Five different ornamentation types of the spores (verrucate, clavate-gemmate, baculate, clavate and baculate-clavate) were determined in the study (Figs. 1-5, Table 4). Different spore types of bryophytes and especially ornamentation patterns of spores play an important role in taxonomically distinguishing between families (Khoshravesh and Kazempour Osaloo, 2007). In addition, some relationships between spore surface ornamentations and substrate surfaces on which bryophytes grow have been reported (Khoshravesh and Kazempour Osaloo, 2007; Savaroğlu, 2015; Can Gözcü et al., 2018). Although these ornamentations of spore surfaces in bryophytes are not for clinging to any pollinator as in pollen grains of flowering plants, they are effective in adhering and settling on the substrate surface.

As a result, palynological studies on bryophyte spores will contribute to both their taxonomy and understanding the mystery of the existence of these primitive plants from the past to the present, ecologically.

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