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The palynological study of some *Hypericum* taxa and its systematic significance

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ABSTRACT: To expose their characteristics and assess their systematic relevance, the palynomorphology of 30 taxa belonging to the *Hypericum* genus (21 species, four subspecies, and five varieties), of which five are endemic, were examined using light and scanning electron microscopy. The studied *Hypericum* taxa pollen grains were monads; isopolar or heteropolar; small to medium size; oblate-spheroidal, prolate-spheroidal, subprolate, spheroidal, and prolate in shape. It was shown that over 20% of the pollen observed (i.e., 13 taxa) was irregular (syncolp(or)ate, pantocolp(or)ate) in terms of aperture number and configuration. The remaining 17 taxa had only 3-colp(or)ate grains typical of the genus. The analyzed taxa were grouped into four categories based on exine sculpturing: microreticulate, microreticulate-perforate, reticulate, and reticulate-perforate. Moreover, four distinct taxonomic groupings were shown due to the UPGMA cluster analysis made to evaluate the morphological characteristics of the studied taxa's pollen. Additionally, due to a PCA ordination, pollen diameter, colpus length, and mesocolpia played significant roles in the ordination and confirmed the patterns found in the cluster analysis. The findings presented here contribute to the palynomorphological information on the genus *Hypericum*, which is crucial for taxonomy. Furthermore, pollen morphology, particularly aperture types, has proven to be a helpful diagnostic trait in the *Hypericum* genus.

KEY WORDS: Hypericaceae, *Hypericum*, pollen morphology, UPGMA, Turkey.

INTRODUCTION

Hypericum L. is one of the biggest 100 angiosperm genera in the world from Hypericaceae Juss., with about 500 species of trees, shrubs, and herbs (Robson, 2012; Meseguer and Sanmartin, 2012). They are found throughout the Mediterranean Basin, particularly in Turkey and the surrounding areas, but not in Antarctica, deserts, or tropical lowlands, and exhibit noteworthy morphological and phytochemical variety (Robson, 2003; Nurk and Crockett, 2011; Otaghvari *et al.,* 2015). The genus has been divided into 36 taxonomic divisions due to a series of monograph studies, the first made by Robson in 1977. However, the taxonomic classification of the *Hypericum* has been long debated, with *Hypericum* commonly categorized as either a tribe or a subfamily under the broadly defined Clusiaceae family (Robson, 1977; Crockett and Robson, 2011; Meseguer and Sanmartin, 2012). According to the most recent taxonomic studies, *Hypericum* belongs to the family Hypericaceae as a genus, and the three tribes in this family are the tropical Cratoxyleae (*Eliea* and *Cratoxylon*) and Vismieae (*Harungana, Vismia,* and *Psorospermum*) and the nearly worldwide Hypericeae Juss (*Hypericum, Triadenum, Thornea, Santomasia, and Lianthus*) (Stevens, 2007; Nürk and Blatner, 2010; Crockett and Robson, 2011). The genus *Hypericum* (Hypericaceae) makes up about 80% of the variety (Robson, 1977, 2012). Kato, (1985) also indicated that the genus *Hypericum* is extremely diverse, posing numerous taxonomic issues at the species level. In addition, Robson, (1990) could not identify the infraspecific classification of many specimens. Additionally, Jenfaoui *et al.,* (2021) stated that identifying the *Hypericum* species has significant morphological variability, and their identification based on vegetative stage distinctions may be problematic. Recent phylogenetic studies based on morphological and molecular characteristics have shown that the genus *Hypericum* is not monophyletic (Nürk and Blattner, 2010; Rhufel *et al.,* 2011; Meseguer and Sanmartín, 2012).

Pollen morphology has become an important tool for resolving various taxonomic issues at the family, generic, or specific level, and numerous scientific studies in systematic botany, paleobotany, paleoecology, etc., can employ the knowledge of pollen morphology and classification as an instrument (Mazari *et al.,* 2017; Gabr, 2018). The fundamental research on the pollen of the Hypericaceae was primarily documented by Erdtman in 1952 and Aytug *et al.,* in 1971. Then, other authors published diverse pollen morphology data for the genus *Hypericum* (Khan, 1969; Clarke, 1975, 1976, 1981; Martonfi *et al.,* 2002; Meseguer and Sanmartin, 2012; Faghir *et al.,* 2018). However, studies on the pollen morphology of the *Hypericum* taxa from Turkey need to be better documented in the literature. Robson (1967) reviewed the Hypericum genus in the Flora of Turkey and the East Aegean Islands, where 84 taxa were examined under 19 sections. Many new taxa from Turkey have been

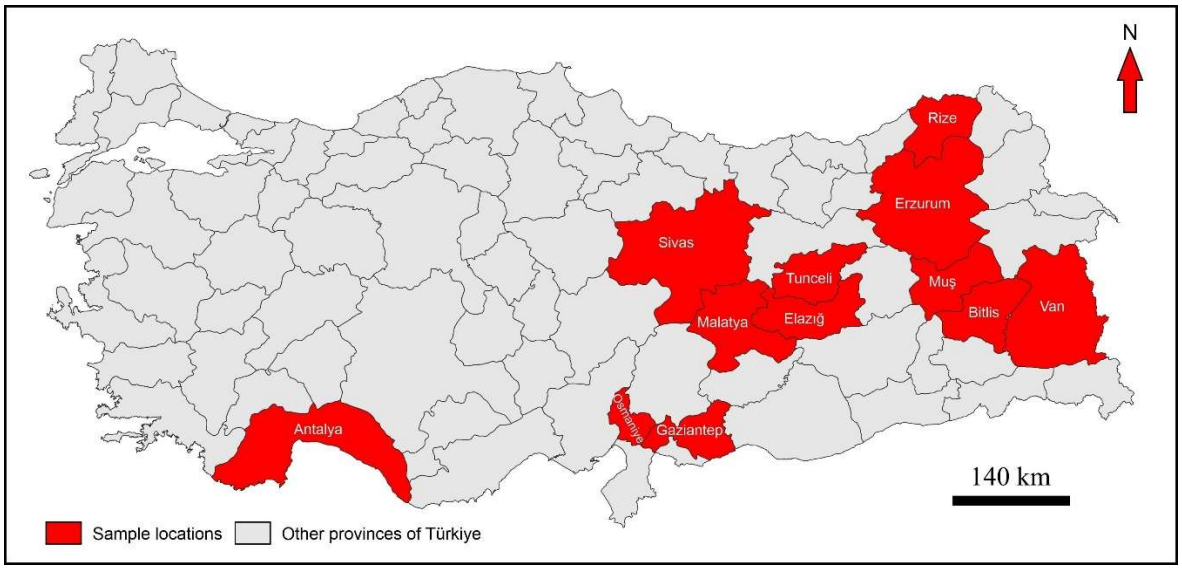

Fig. 1. Location map where plant samples were collected (modified from Ekinci *et al.,* 2020).

described since then (Ozbek *et al.,* 2019). This genus is now represented in Turkey by 20 sections and 119 taxa, 49 of which are endemic, and Turkey is a prominent gene center for the *Hypericum* taxa (Yuce-Babacan *et al*., 2017; Ozbek *et al.,* 2019; Cosge-Senkal and Uskutoglu, 2021). In this paper, the palynomorphological traits of 30 taxa, five of which are endemic (*H. scabroides, H. sorgerae, H. ekerii, H. thymopsis,* and *H. uniglandulosum*), of the *Hypericum* taxa found in Turkey were analyzed. Pollen grains of the *Hypericum* were examined using light microscopy (LM) and scanning electron microscopy (SEM) to ascertain their palynological characteristics, analyze the systematic importance of traits, and contribute to its systematics by offering helpful data.

MATERIALS AND METHODS

Plant Materials

Plant samples from 30 taxa (21 species, four subspecies, and five varieties) were collected during their flowering phases (June-August) from their type localities and other regions of Turkey (Table 1; Fig. 1). The flowering part of the plants was taken into envelopes and dried. Samples were prepared by taking the anthers from flowers and placing them directly on slides. Some samples were taken from the Firat University Herbarium (FUH) and the Van Yuzuncu Yil University Herbarium (VANF). This study attempted to identify the pollen morphology of species collected from various locations, particularly in eastern Anatolia. As a result, this study will help research that will determine the pollen morphology of taxa to be collected from various locations in Turkey, which is considered a major gene center for *Hypericum*. Several species were included here to support the systematic research of the genus *Hypericum*. The studied samples are kept in the Bitlis Eren University Herbarium (BEUH), Turkey. This research includes taxa belonging to the following sections: Sect. *Androsaemum* (*H. hircinum*), Sect. *Crossophyllum* (*H. orientale*), Sect. *Origanifolia* (*H. origanifolium*), Sect. *Drosocarpium* (*H. montbretii* and *H. bithynicum*), Sect. *Hypericum* (*H. tetrapterum* var. *tetrapterum*, *H. perforatum* subsp. *perforatum*, and *H. triquetrifolium*), Sect. *Taeniocarpium* (*H. confertum* subsp. *stenobotrys*, *H. venustum*, *H. linarioides* subsp. *linarioides*, and *H. armenum* subsp. *armenum*), and Sect. *Hirtella* (other taxa). The plant was ordered in accordance with the Flora of Türkiye (Robson, 1967; 1988).

Palynomorphological Analysis

The pollen morphology of *Hypericum* taxa was examined using light microscopy (LM) and scanning electron microscopy (SEM). Pollen obtained from dried samples was prepared following Wodehouse, (1935). Pollen characteristics were observed in an Olympus BX-31 light microscope at 1000X magnification, and pictures were taken with a digital camera. The variables observed or measured were polar axis (P), equatorial diameter (E), pollen shape (P/E), porus length (Plg), porus width (Plt), colpus length (Clg), colpus width (Clt), exine thickness (Ex), mesocolpia (L), apocolpia (t), intine thickness (In) and ornamentation (Orn) as well as pore shape, polarity, pollen aperturate, and regular or irregular pollen grains. Measurements were made for each pollen morphological trait in at least 30-35 pollen grains per specimen (Table 2). Analysis was carried out in the Biology Department at Bitlis Eren University's Science and Art Faculty.

At the SEM Laboratory of the Central Research Laboratory (MERLAB), Yuzuncu Yil University, Van, non-acetolyzed pollen grains were directly placed onto stubs, sputter-coated with gold, and studied with a ZEISS Supra 55 Scanning Electron Microscope. For pollen terminology, Moore *et al.,* (1991), Faegri and Iversen,

Table 1. The collection data of investigated ***Hypericum*** specimens.

Taxa	Locality, voucher and specimen code
Sect. *Androsaemum*	
H. hircinum L.	Gaziantep province, İslahiye district, Koccağız village, 1020 m, 19.06.2006, *S. Çakır 902*.
Sect. *Hirtella*	
H. spectabile Jaub. & Spach	Gaziantep province, İslahiye district, Alaca village, 750 m, 27.05.2007, *S. Çakır 1407*.
H. lysimachiodes Boiss.& Noë var. *lysimachiodes*	Van province, Kuzgun Kıran pass, 1800 m, 14.06.2022, *M. Kürşat 7068*.
H. lysimachiodes var. spathulatum N.Robson	Bitlis province, Kambos mountain, 1750 m, 16.07.2022. *M. Kürşat 7063*
H. elongatum Ledeb. ex Rchb. var. *elongatum*	Elazığ province, Baskil district, Doğançık village, 1800 m, 03.06.2021, *M. Kürşat 7076*.
H. elongatum var. *antasiaticum* (Grossh.) N.Robson	Van province, Güzeldere pass, Western slope, 2600m, 04.07.20022, *M. Kürşat 7082*.
H. karjaginii Rzazade	Sivas province, Between Hekimhan and Kangal district, 38.km, 1500-1600 m, 30.06.2008, *E. Yüce 1096*.
H. microcalycinum Boiss. & Heldr.	Elazığ province, Baskil district, Haroğlu Village, 1450 m. 03.06.2021, *M. Kürşat 7072*.
H. sorgerae N.Robson	Sivas province, Between Sivas and Zara district, 20 km, 1500 m, 29.06.2008, *E. Yüce 1088*.
H. davisii N.Robson	Van province, Güzeldere pass, Eastern slope, 2700 m, 04.07.20022, *M. Kürşat 7083*.
H. lydium Boiss.	Van province, Peli mountain, 2700 m, 14.06.2021, *M. Kürşat 7070*.
H. pseudolaeve N.Robson	Malatya province, Between Malatya and Gölbaşı district, 50.km, 860 m, 02.06.2008, *E.Yüce 1052*.
H. helianthemoides (Spach) Boiss.	Van province, Van-Gürpınar district fork in the road, Koyunyatağı village, 1750 m, 04.07.2022, *M. Kürşat 7085*.
H. thymbrifolium Boiss. & Noë	Malatya province, Between Malatya and Darende district, 50. km, 1500 m, 29.06.2008, *E.Yüce 1084*.
H. uniglandulosum Hausskn. ex Bornm.	Elazığ province, Hasan mountain, 2100 m, 28.07.2022, *M. Kürşat 7073*.
H. ekerii Yüce & Aytaç	Tunceli province, Mazgirt district, c. 21 km E of Tunceli, c. 3 km SE of Çevrecik, Munzur Mountain ranges, 1800–2060 m, 11.06.2015, *E.Yüce 2246*.
H. scabroides N.Robson & Poulter	Elazığ province, Baskil district, Doğançık Village, around Bolucuk town, 1480 m, 03.06.2021, *M. Kürşat 7074*.
H. scabrum L.	Elazığ province, Baskil district, Doğançık Village, around Bolucuk town, 1530 m, 03.06.2021, *M. Kürşat 7075*.
H. thymopsis Boiss	Sivas province, Gürün district, Gökpınar village, 1600 m, 05.07.2021, *M. Kürşat 7093*.
Sect. *Taeniocarpium*	
H. confertum subsp. *stenobotrys* (Boiss.) Holmboe	Gaziantep province, İslahiye district, Köklü village, 840 m, 22.04.2006, S. Çakır 460.
H. venustum Fenzl	Bitlis; Tatvan district and Van, 15. km, 1900 m, 09.07.2021, *M. Kürşat 7066*.
H. linarioides Bosse subsp. *linarioides*	Erzurum province, Şenkaya district, Gülvere village, 2500 m, 20.08.1980, *Y. Altan 2913*.
H. armenum Jaub. & Spach subsp. *armenum*	Muş province, Kurtik mountain, 2450 m, 27.04.2018, *M. Kürşat 7056*.
Sect. *Drosocarpium*	
H. montbretii Spach	Osmaniye province, Zorkun plateau, in the Forest, 1650 m, 22.06.2021, *M. Kürşat 7059*.
H. bithynicum Boiss.	Rize province, Çamlıhemşin district, Between Ortayayla village and Başköy village, Wetland,, 2100 m, 01.07.2021, *M. Kürşat 7067*.
Sect. *Crossophyllum*	
H. orientale L.	Rize province, Çamlıhemşin district, Between Ortayayla village and Başköy village, Wetlands, 2160 m, 01.07.2021, *M. Kürşat 7060*.
Sect. *Origanifolia*	
H. origanifolium Willd.	Antalya province, Akseki district, Sadıklar village, 1050-1250 m, 14.05.1995, *A. Duran 2387*.
Sect. *Hypericum*	
H. tetrapterum Fr. var. *tetrapterum*	Malatya province, Kubbe mountain, stream, 2000 m, 29.07.1981, *Y. Altan 1962*.
H. perforatum L. subsp. *perforatum*	Elazığ province, Baskil district, Doğançık Village, around Bolucuk town, 1530 m, 03.06.2021, *M. Kürşat 7077*.
H. triquetrifolium Turra	Elazığ province, Baskil district, 1300 m, 28.07.2021, *M. Kürşat 7065*.

Table 2. Pollen morphological data for the ***Hypericum*** taxa (µm) (medium ± standard deviation).

Taxa	P	E	P/E	Clg	Clt	Plg	Plt	Ex	In	t	L
Hypericum hircinum	20.05±0.88	19.87±0.94	O-s	17.18±1.01	3.60±0.52	5.80±0.59	5.78±0.60	1.11±0.13	0.57±0.11	3.22±0.73	19.67±1.23
H. spectabile	21.97±1.40	18.02±1.62	S	18.67±1.08	2.43±1.19	---	---	1.38±0.30	0.66±0.18	---	----
H. lysimachioides var. *lysimachioides*	26.43±1.22	22.87±1.33	S	21.33±1.47	4.27±0.75	5.90±0.74	5.75±0.73	1.66±0.37	0.70±0.26	2.81±0.64	23.53±1.53
H. lysimachioides var. *spathulatum*	25.34±1.50	23.03±2.12	Sf	22.09±1.16	4.03±0.74	6.86±1.32	6.58±1.31	1.48±0.19	0.68±0.19	3.03±1.25	24.77±1.61
H. elongatum var. *elongatum*	23.10±1.65	22.03±1.56	P-s	19.73±2.20	3.78±0.66	4.27±0.60	4.07±0.56	1.43±0.20	0.53±0.17	2.65±0.54	21.30±1.37
H. elongatum var. *antasiaticum*	24.03±1.30	23.43±1.19	P-s	---	---	---	---	1.35±0.18	0.53±0.14	---	---
H. karjaginii	24.70±1.58	23.97±1.63	P-s	---	---	---	---	1.18±0.21	0.73±0.19	---	---
H. microcalycinum	14.90±0.66	13.40±0.97	P-s	12.93±0.99	3.09±0.53	5.17±0.66	4.97±0.77	0.86±0.19	0.43±0.16	2.36±0.58	13.83±1.53
H. sorgerae	23.03±1.38	22.77±1.63	P-s	---	---	5.28±0.71	5.10±0.98	1.02±0.16	0.52±0.13	---	---
H. davisii	22.97±1.85	22.60±1.34	P-s	---	---	---	---	1.12±0.26	0.65±0.19	---	---
H. lydium	22.43±1.48	20.06±1.28	Sf	19.47±1.13	5.87±0.71	5.20±0.70	5.08±0.96	1.53±0.17	0.62±0.11	4.70±0.74	21.06±1.71
H. pseudolaeve	15.43±1.43	13.98±1.36	P-s	13.10±1.30	2.90±0.49	5.00±0.63	4.68±0.51	0.74±0.28	0.54±0.09	2.41±0.40	14.03±1.16
H. helianthemoides	23.90±1.26	23.08±1.35	P-s	---	---	5.38±0.73	5.42±0.83	1.15±0.18	0.65±0.18	---	---
H. thymbrifolium	18.62±1.10	16.73±0.76	P-s	16.08±0.96	4.07±0.86	6.23±0.79	6.15±1.03	0.88±0.22	0.53±0.14	2.76±0.53	16.80±0.96
H. uniglandulosum	17.97±1.25	15.77±1.01	Sf	15.27±1.96	4.61±0.55	6.51±0.74	6.40±0.72	1.23±0.20	0.45±0.15	3.00±0.66	16.20±1.47
H. ekerii	14.42±1.40	11.95±0.71	S	12.17±0.82	1.53±0.33	3.74±0.32	2.56±0.33	1.44±0.33	0.63±0.18	2.04±0.47	12.47±0.94
H. scabroides	21.37±2.03	20.83±1.98	P-s	---	---	5.25±0.65	5.10±0.68	1.70±0.26	0.72±0.19	---	---
H. scabrum	21.07±1.20	19.93±1.37	O-s	14.73±1.44	3.28±0.84	4.93±0.61	4.59±0.54	1.51±0.19	0.60±0.17	2.53±0.54	20.04±1.59
H. thymopsis	15.93±1.24	13.67±1.37	Sf	13.83±1.11	2.83±0.46	3.86±0.57	3.58±0.59	0.63±0.19	0.50±0.11	2.70±0.41	13.37±1.17
H. confertum ssp. *stenobotrys*	17.70±0.62	15.35±0.77	S	15.67±0.85	4.15±0.54	5.37±0.80	5.12±0.83	0.89±0.20	0.47±0.13	2.58±0.55	15.47±0.97
H. venustum	24.10±1.68	18.05±0.70	Pr	20.87±2.52	3.90±0.88	---	---	0.98±0.14	0.53±0.15	2.57±0.58	19.13±1.01
H. linarioides ssp. *linarioides*	21.17±1.38	15.20±1.28	Pr	18.95±1.32	3.75±0.54	5.41±0.57	5.26±0.54	0.75±0.15	0.48±0.14	2.95±0.76	16.50±1.15
H. armenum ssp. *armenum*	19.30±1.06	17.76±1.28	P-s	15.66±1.47	4.67±0.59	6.75±0.67	6.51±0.63	1.49±0.63	0.58±0.17	2.55±0.53	18.10±1.97
H. montbretii	19.03±1.13	16.38±0.69	Pr	13.62±1.13	5.18±0.89	6.33±0.84	6.21±1.10	1.76±0.28	0.46±0.11	4.03±0.73	20.58±1.70
H. bithynicum	22.72±1.40	16.55±0.99	Pr	20.40±1.99	3.28±0.58	---	---	1.41±0.23	0.66±0.19	2.19±0.38	18.93±1.78
H. orientale	20.37±1.59	17.77±1.50	S	17.07±1.72	3.10±0.62	5.18±0.74	5.02±0.74	1.27±0.17	0.60±0.16	2.18±0.44	19.57±1.07
H. origanifolium	19.87±1.87	15.85±0.71	S	17.70±1.86	4.15±0.59	6.48±0.59	6.13±0.86	1.10±0.13	0.56±0.11	2.83±0.61	16.87±1.20
H. tetrapterum var. *tetrapterum*	17.23±1.63	16.90±2.30	P-s	14.77±1.96	2.82±0.52	5.40±0.96	5.09±0.49	1.13±0.18	0.47±0.08	2.53±0.54	16.90±1.32
H. perforatum ssp. *perforatum*	19.17±1.37	16.13±1.28	S	16.20±1.74	4.23±0.57	5.35±0.74	5.01±0.69	1.18±0.28	0.45±0.17	3.82±0.61	16.67±0.99
H. triquetrifolium	19.87±1.83	16.90±1.72	S	16.37±1.65	3.61±0.50	5.75±0.52	5.46±0.41	1.28±0.21	0.58±0.11	3.86±0.74	18.40±1.16

Abbreviations: (P): Polar axis, **(E):** equatorial diameter, **(P/E):** Pollen shape, **(Plg):** pore length, **(Plt):** pore width, **(Clg):** colpus length **(Clt):** colpus width, **(Ex):** exine thickness **(L):** mesocolpia **(t):** apocolpia **(In):** Intine thickness, **(O-s):** Oblate-spheroidal, **(P-s):** prolate-spheroidal, **(S):** Subprolate, **(Sf):** Spheroidal, **(Pr):** Prolate,

(1992), and Punt *et al.,* (2007) were followed. The class of pollen shape, based partly on the P/E ratio, was determined following Erdtman's system, (Erdtman, 1969).

Statistical Analyses

Statistical analyses were carried out using the palynomorphological characteristics collected from the 30 taxa (Tables 2 & 3). An unweighted pair group technique with arithmetic mean (UPGMA) clustering was done with the multi-variate statistical analyses software (MVSP) to group taxa concerning morphological similarities and pinpoint taxa relationships. This was followed by a principal component analysis (PCA) to know the variables' contribution to the ordination/clustering obtained (Kovach, 1999).

RESULTS

The quantitative and qualitative characteristics of *Hypericum* pollen grains are shown in Tables 2, 3, 4. Based on the LM and SEM micrographs, the *Hypericum* taxa's micromorphological characteristics are described in detail (Tables 2, 3, 4; Figs. 2–6).

Table 3. SEM analysis data of the examined ***Hypericum*** taxa

Taxa	Polarity	Pore shape	Pollen aperturate	Pollen regular/irregular	Ornamentation
H. hircinum	isopolar	lalongate and circular	3-colporate	Regular	Microreticulate-perforate
H. spectabile	isopolar, heteropolar	lolongate	3-colp(or)ate, 6-pantocolpate, 4-syncolporate	Regular-irregular	Reticulate-perforate
H. lysimachioides var. *lysimachioides*	isopolar, heteropolar	lalongate	3-colporate, 4-colp(or)ate, 6-pantocolporate, 6-syncolporate	Regular-irregular	Microreticulate
H. lysimachioides var. *spathulatum*	isopolar, heteropolar	lalongate	3-colporate, 4-colp(or)ate, 6-pantocolporate	Regular-irregular	Microreticulate-perforate
H. elongatum var. *elongatum*	isopolar, heteropolar	lalongate and circular	3-colporate, 4-colp(or)ate, (6)-(12)-pantocolporate, 4-syncolp(or)ate, (3)-(8)-syncolporate	Regular-irregular	Microreticulate
H. elongatum var. *antasiaticum*	isopolar, heteropolar	lolongate and lalongate	3-colporate, 4-colp(or)ate, (6)-(12)-pantocolp(or)ate, 3-syncolporate, (4)-(6)-syncolpate	Regular-irregular	Microreticulate-perforate
H. karjaginii	heteropolar	lalongate	6-syncolporate, 6-syncolpate (6)-(12)-pantocolporate	Irregular	Microreticulate-perforate
H. microcalycinum	isopolar	lalongate	3-colp(or)ate	Regular	Microreticulate-perforate
H. sorgerae	isopolar, heteropolar	lalongate and circular	3-colporate, 6-pantocolporate (3)-(4)-syncolpate	Regular-irregular	Reticulate-perforate
H. davisii	isopolar, heteropolar	lolongate	4-colpate, 6-pantocolporate, 4-syncolp(or)ate	Regular-irregular	Microreticulate-perforate
H. lydium	isopolar, heteropolar	lalongate	3-colporate, 4-colpate, 4-syncolporate	Regular-irregular	Microreticulate-perforate
H. pseudolaeve	isopolar	lolongate and lalongate	3-colp(or)ate	Regular	Microreticulate-perforate
H. helianthemoides	heteropolar	lalongate	6-pantocolporate, (4)-(6)-syncolporate,	Irregular	Microreticulate-perforate
H. thymbrifolium	isopolar	lalongate	3-colp(or)ate	Regular	Reticulate-perforate
H. uniglandulosum	isopolar	circular	3-colporate	Regular	Microreticulate-perforate
H. ekerii	isopolar	lolongate	3-colp(or)ate	Regular	Microreticulate-perforate
H. scabroides	isopolar, heteropolar	lalongate	(3)-(4)-colpate, (4)-(6)-syncolpate,	Regular-irregular	Microreticulate-perforate
H. scabrum	isopolar, heteropolar	lalongate	3-colporate, 12-pantocolp(or)ate, (3)-(6)-syncolpate, (4)-syncolp(or)ate	Regular-irregular	Reticulate
H. thymopsis	isopolar	lalongate	3-colp(or)ate	Regular	Reticulate
H. confertum subsp. *stenobotrys*	isopolar	lalongate and circular	3-colp(or)ate,	Regular	Microreticulate
H. venustum	isopolar	lalongate	3-colp(or)ate	Regular	Microreticulate-perforate
H. linarioides subsp. *linarioides*	isopolar	lolongate	3-colp(or)ate	Regular	Microreticulate
H. armenum subsp. *armenum*	isopolar	lalongate	3-colp(or)ate	Regular	Reticulate
H. montbretii	isopolar	lolongate	3-colp(or)ate	Regular	Microreticulate-perforate
H. bithynicum	isopolar	lolongate	3-colp(or)ate	Regular	Reticulate
H. orientale	isopolar	lolongate	3-colporate	Regular	Microreticulate
H. origanifolium	isopolar	lolongate and lalongate	3-colp(or)ate	Regular	Microreticulate-perforate
H. tetrapterum var. *tetrapterum*	isopolar	lalongate	3-colporate	Regular	Microreticulate-perforate
H. perforatum subsp. *perforatum*	isopolar, heteropolar	lalongate	3-colporate, (3)-(4)-(6)-syncolpate,	Regular-irregular	Microreticulate-perforate
H. triquetrifolium	isopolar	lalongate	3-colp(or)ate	Regular	Microreticulate-perforate

Table 4. Micromorphological characteristics of distinctive taxa in the sections of the genus ***Hypericum***.

Section	Pollen regular/irregular	Polarity	Pore shape	Pollen aperturate	Ornamentation
Androsaemum	Regular	Isopolar	Lalongate, Circular	3-colporate	Microreticulate-perforate
Hirtella	Regular, Irregular	Isopolar, Heteropolar	Lalongate, Lolongate, Circular	3-4colp(or)ate, (6)-(12)-pantocolp(or)ate, (3)-(4)-(6)-(8)-syncolp(or)ate	Microreticulate-perforate Microreticulate, Reticulate-perforate, Reticulate
Taeniocarpium	Regular	Isopolar	Lalongate, Lolongate, Circular	3-colp(or)ate	Microreticulate-perforate Microreticulate, Reticulate
Drosocarpium	Regular	Isopolar	Lolongate	3-colp(or)ate	Microreticulate-perforate Reticulate
Crossophyllum	Regular	Isopolar	Lolongate	3-colporate	Microreticulate
Origanifolia	Regular	Isopolar	Lolongate, Lalongate	3-colp(or)ate	Microreticulate-perforate
Hypericum	Regular-irregular	Isopolar, Heteropolar	Lalongate	3-colporate, (3)-(4)-(6)-syncolpate	Microreticulate-perforate

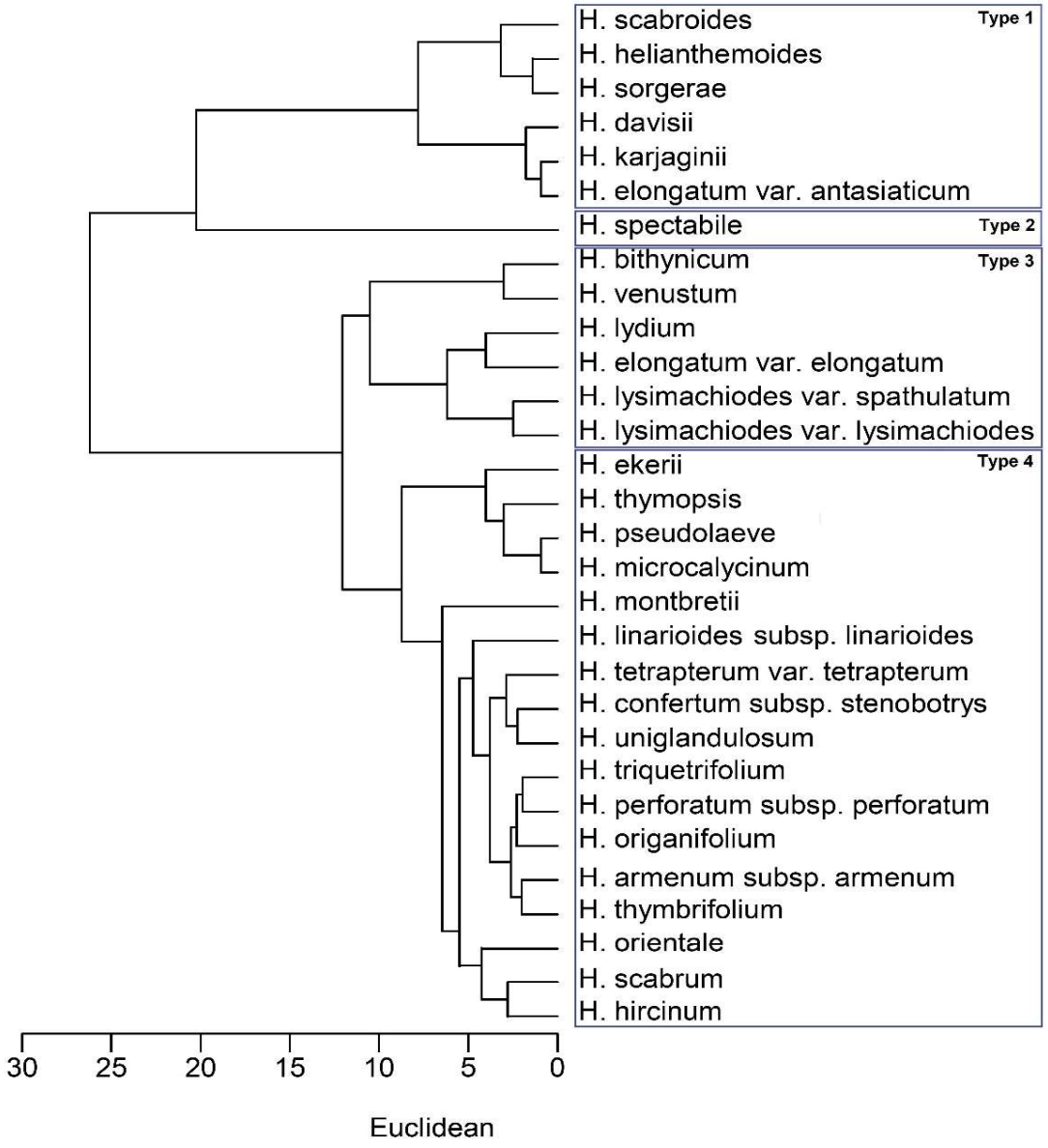

Fig. 2. Dendrogram obtained from the analysis of the pollen morphological character data in the taxa under study and their related taxonomic relationships. **Type 1** included *H. elongatum* var. *antasiaticum*, *H. karjaginii*, *H. sorgerae*, *H. davisii*, *H. helianthemoides,* and *H. scabroides*; **Type 2** included only *H. spectabile*; **Type 3** included *H. lysimachiodes* var. *lysimachiodes*, *H. lysimachiodes* var. *spathulatum*, *H. elongatum* var. *elongatum*, *H. lydium*, *H. venustum,* and *H. bithynicum*; **Type 4** included other subtypes.

Table 5. Pollen morphological parameters analyzed by principal component analysis (PCA).

PCA		Axis 1	Axis 2
Eigenvalues		121.792	19.297
Percentage		75.574	11.974
Cumulative Percentage		75.574	87.548
PCA variable loadings			
Morphological parameters	**Characters**	**Axis 1**	**Axis 2**
Polarity	Pol	-0.058	0.098
Polar axis	P	-0.062	0.693
Equatorial diameter	E	-0.139	0.668
Colpus longitude (length)	Clg	0.629	0.113
Colpus latitude (width)	Clt	0.144	-0.012
Porus length	Plg	0.099	-0.130
Porus width	Plt	0.094	-0.104
Exine thickness	Ex	0.002	0.030
Intine thickness	In	-0.002	0.010
Apocolpia	t	0.111	-0.041
Mesocolpia	L	0.726	0.136
Ornamentation	Orn	-0.006	-0.029
Pore shape	Ps	0.008	0.027

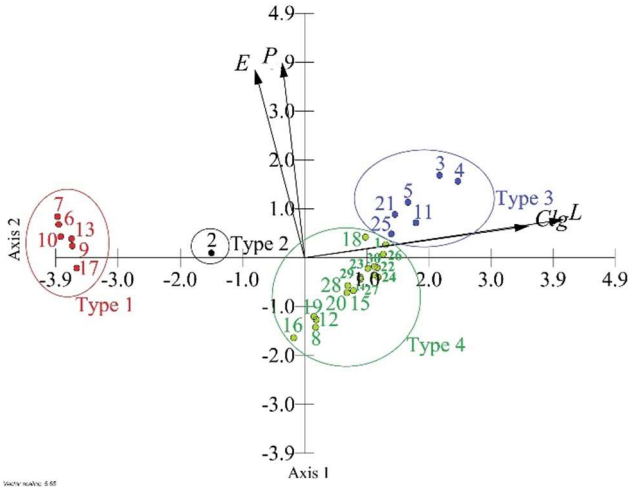

Fig. 3. Principal component analysis scatter plot obtained from the overlapping of taxa. **1.** *H. hircinum*, **2.** *H. spectabile*, **3.** *H. lysimachioides* var. *lysimachioides*, **4.** *H. lysimachioides* var. *spathulatum*, **5.** *H. elongatum* var. *elongatum*, **6.** *H. elongatum* var. *antasiaticum*, 7. *H. karjaginii*, **8.** *H. microcalycinum*, **9.** *H. sorgerae*, **10.** *H. davisii*, **11.** *H. lydium*, **12.** *H. pseudolaeve*, **13.** *H. helianthemoides*, **14.** *H. thymbrifolium*, **15.** *H. uniglandulosum*, **16.** *H. ekerii*, **17.** *H. scabroides*, **18.** *H. scabrum*, **19.** *H. thymopsis*, **20.** *H. confertum* subsp. *stenobotrys*, **21.** *H. venustum*, **22.** *H. linarioides* subsp. *linarioides*, **23.** *H. armenum* subsp. *armenum*, **24.** *H. montbretii*, **25.** *H. bithynicum*, **26.** *H. orientale*, **27.** *H. origanifolium*, **28.** *H. tetrapterum* var. *tetrapterum*, **29.** *H. perforatum* subsp. *perforatum*, **30.** *H. triquetrifolium*, Clg: colpus length, L: mesocolpia, P: polar axis and E: equatorial diameter.

Pollen Morphology

The *Hypericum* taxa had oblate-spheroidal, prolate-spheroidal, subprolate, spheroidal, and prolate pollen shapes being isopolar, heteropolar, and isopolar-heteropolar. The pollen grains were small to medium, with a polar axis length between 14.42 to 26.43 µm and an equatorial diameter of 11.95 to 23.97 µm. *H. ekerii* was the smallest pollen grain (11.95–14.42µm), whereas *H. lysimachioides* var. *lysimachioides* was the largest one (22.87–26.43µm) (Tables 2 & 3; Figs. 4–6).

Most *Hypericum* taxa have tricolp(or)ate, 4-colp(or)ate, syncolp(or)ate, and pantocolp(or)ate pollen grains (Table 3). It was also found that the colpus of the studied genus is short to somewhat long (12.17–21.33 µm), narrow (1.53–5.87 µm), with acute ends. The colpus edges are also clearly defined. The pore dimensions were 3.74 to 6.86 µm long and 2.56 to 6.58 µm wide. The thickness of apocolpia varied from 2.04 to 4.70 µm, while the thickness of mesocolpia varied from 12.47 to 24.77 µm, and the aperture membrane was found to be granulated. The porus shape was lolongate, lalongate, or circular. Examined *Hypericum* taxa had psilate colpus membranes with operculum present (Table 3).

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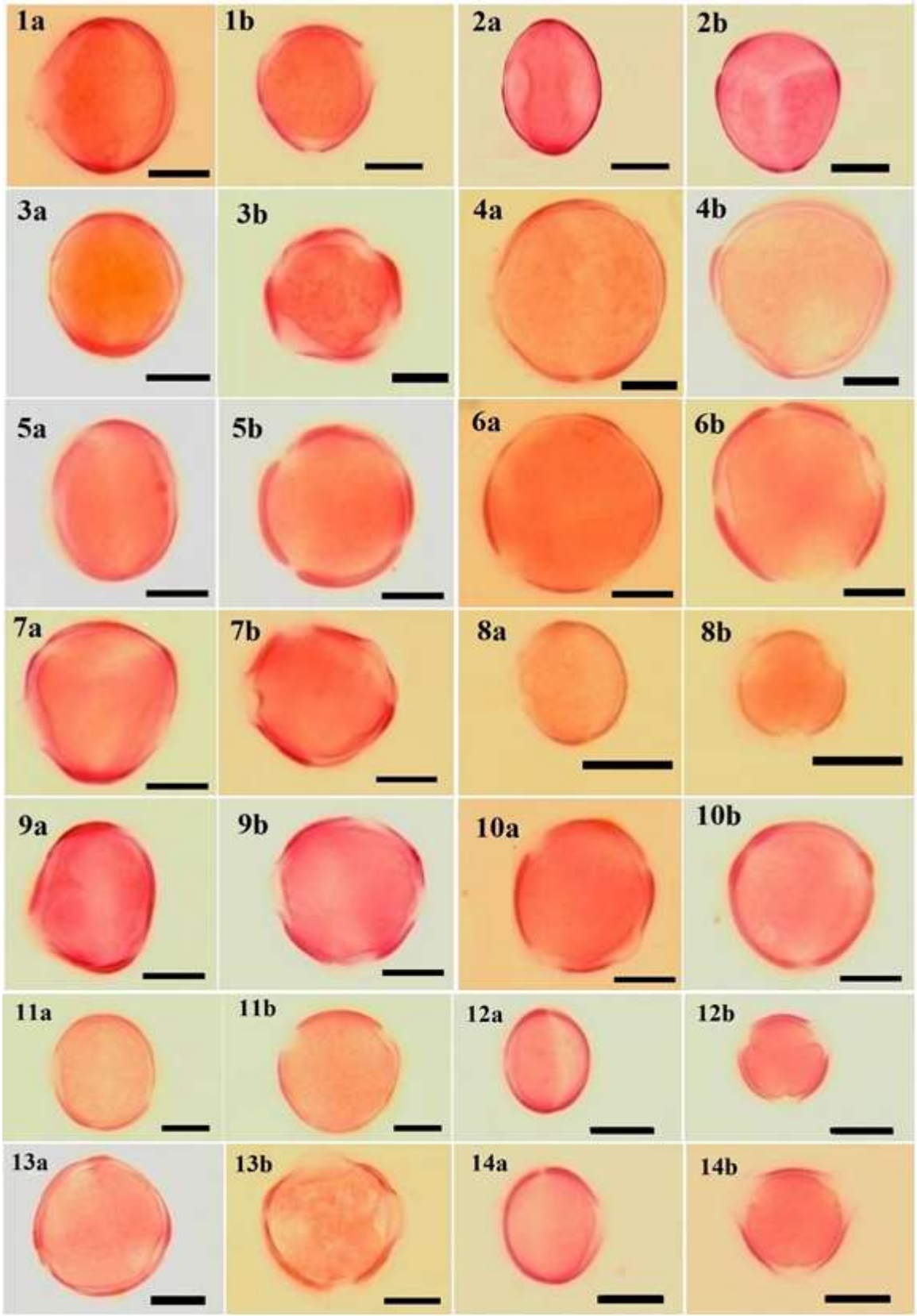
A tectate exine was observed in the analyzed specimens, with a thickness between 0.74–1.76 µm. Additionally, it was found that the ectexine was thicker than the endexine (Table 2). Exine sculpturing is also shown to be microreticulate-perforate, microreticulate, reticulate, and reticulate-perforate (Table 3; Figs. 5 & 6). Also, pollen grains were categorized by size into five classes by Erdtman (1952): very small (10 µm), small (10–25 µm), medium (26–50 µm), large (51–100 µm), and huge (>100 µm).

Cluster analysis and ordination

Fig. 2 shows the results of the cluster analysis. Four types of taxa were defined as type 1 (*H. elongatum* var. *antasiaticum*, *H. karjaginii*, *H. sorgerae*, *H. davisii*, *H. helianthemoides* and *H. scabroides*), type 2 (*H. spectabile*), type 3 (*H. lysimachioides* var. *lysimachioides*, *H. lysimachioides* var. *spathulatum*, *H. elongatum* var. *elongatum*, *H. lydium*, *H. venustum,* and *H. bithynicum*), and type 4 (other taxa) (Fig. 2). The PCA explained 87.5% of the variance, and the ordering obtained agrees with the cluster analyses. (Figs. 2 & 3). Colpus length (Clg) and mesocolpia (L) play a significant role in ordering types 1, 2, and 3. The polar axis (P) and equatorial diameter (E) are inverse in positioning type 4. In other words, type 4 pollen grains are smaller (Table 5; Fig. 3).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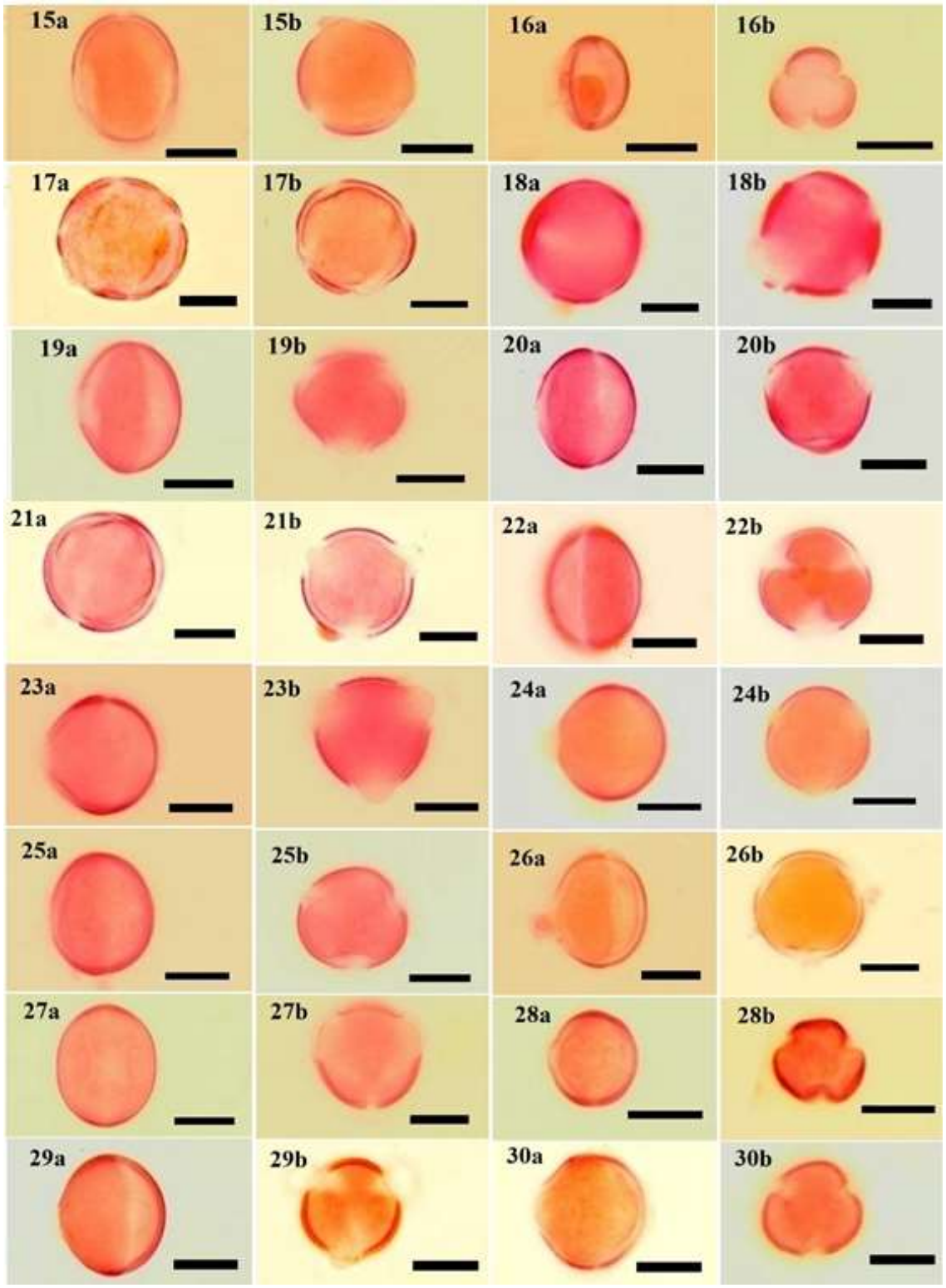
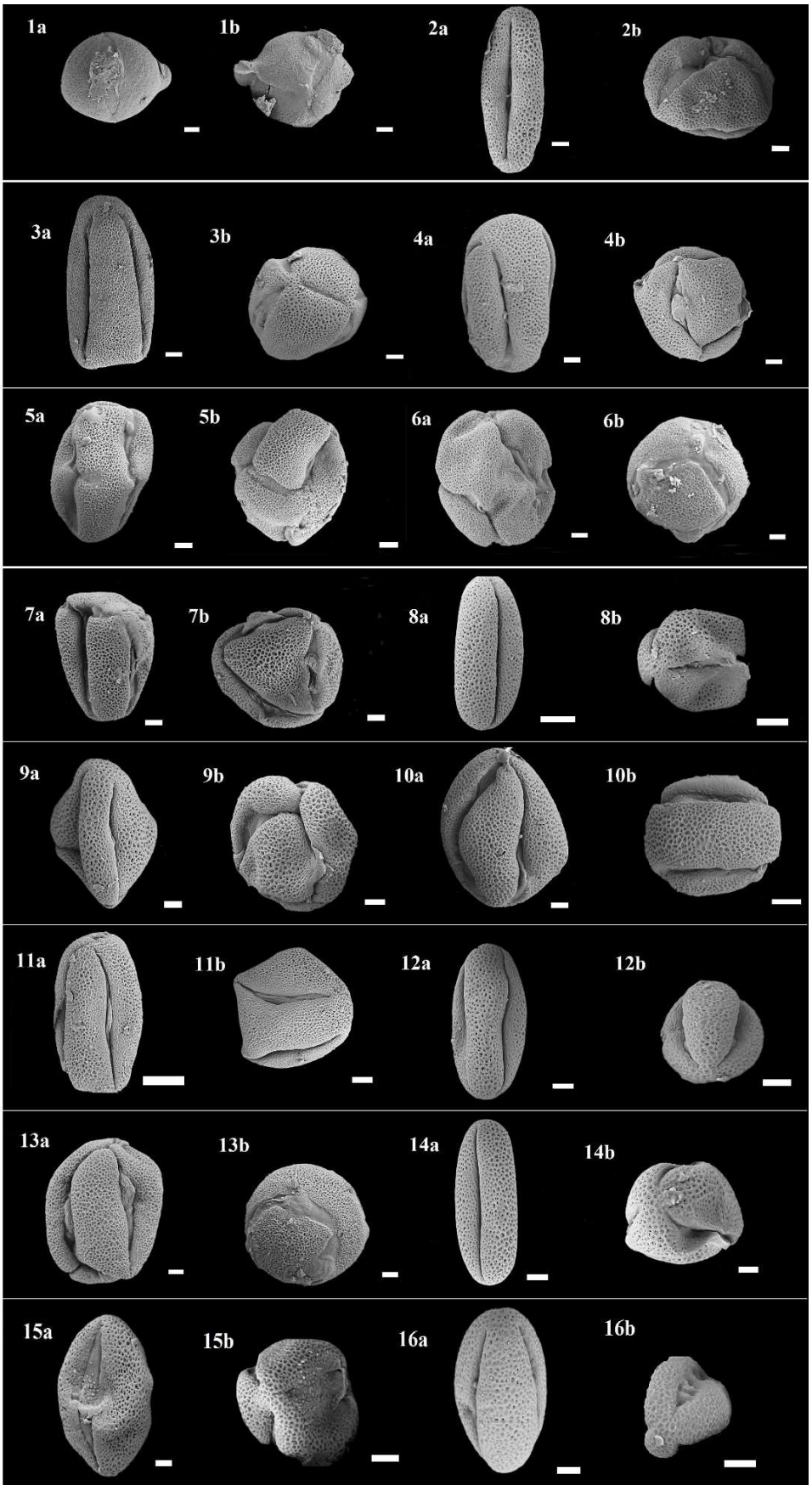


Fig. 4. *Hypericum* by Light Microscopy: **1a-b.** *H. hircinum*, **2a-b.** *H. spectabile*, **3a-b.** *H. lysimachiodes* var. *lysimachiodes*, **4a-b.** *H. lysimachiodes* var. *spathulatum*, **5a-b.** *H. elongatum* var. *elongatum*, **6a-b.** *H. elongatum* var. *antasiaticum*, **7a-b.** *H. karjaginii*, **8a-b.** *H. microcalycinum*, **9a-b.** *H. sorgerae*, **10a-b.** *H. davisii*, **11a-b.** *H. lydium*, **12a-b.** *H. pseudolaeve*, **13a-b.** *H. helianthemoides*, **14a-b.** *H. thymbrifolium*, **15a-b.** *H. uniglandulosum*, **16a-b.** *H. ekerii* **17a-b.** *H. scabroides*, **18a-b.** *H. scabrum,* **19a-b.** *H. thymopsis*, **20a-b.** *H. confertum* subsp. *stenobotrys*, **21a-b.** *H. venustum*, **22a-b.** *H. linarioides* subsp. *linarioides* **23a-b.** *H. armenum* subsp. *armenum* **24a-b.** *H. montbretii,* **25a-b.** *H. bithynicum,* **26a-b.** *H. orientale,* **27a-b.** *H. origanifolium,* **28a-b.** *H. tetrapterum* var. *tetrapterum,* **29a-b.** *H. perforatum* subsp. *perforatum,* **30a-b.** *H. triquetrifolium* **(scale bar 10 µm)**.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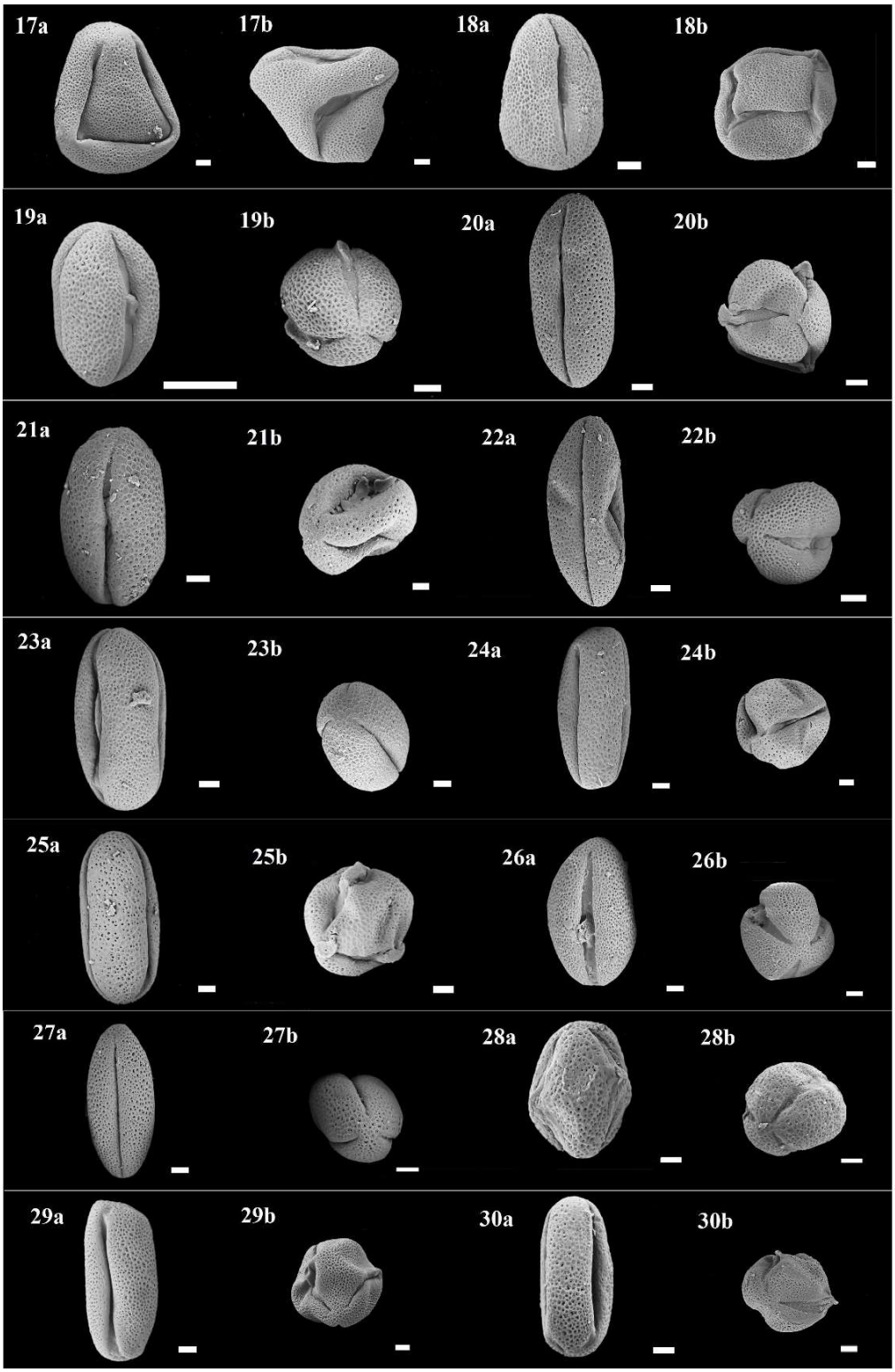
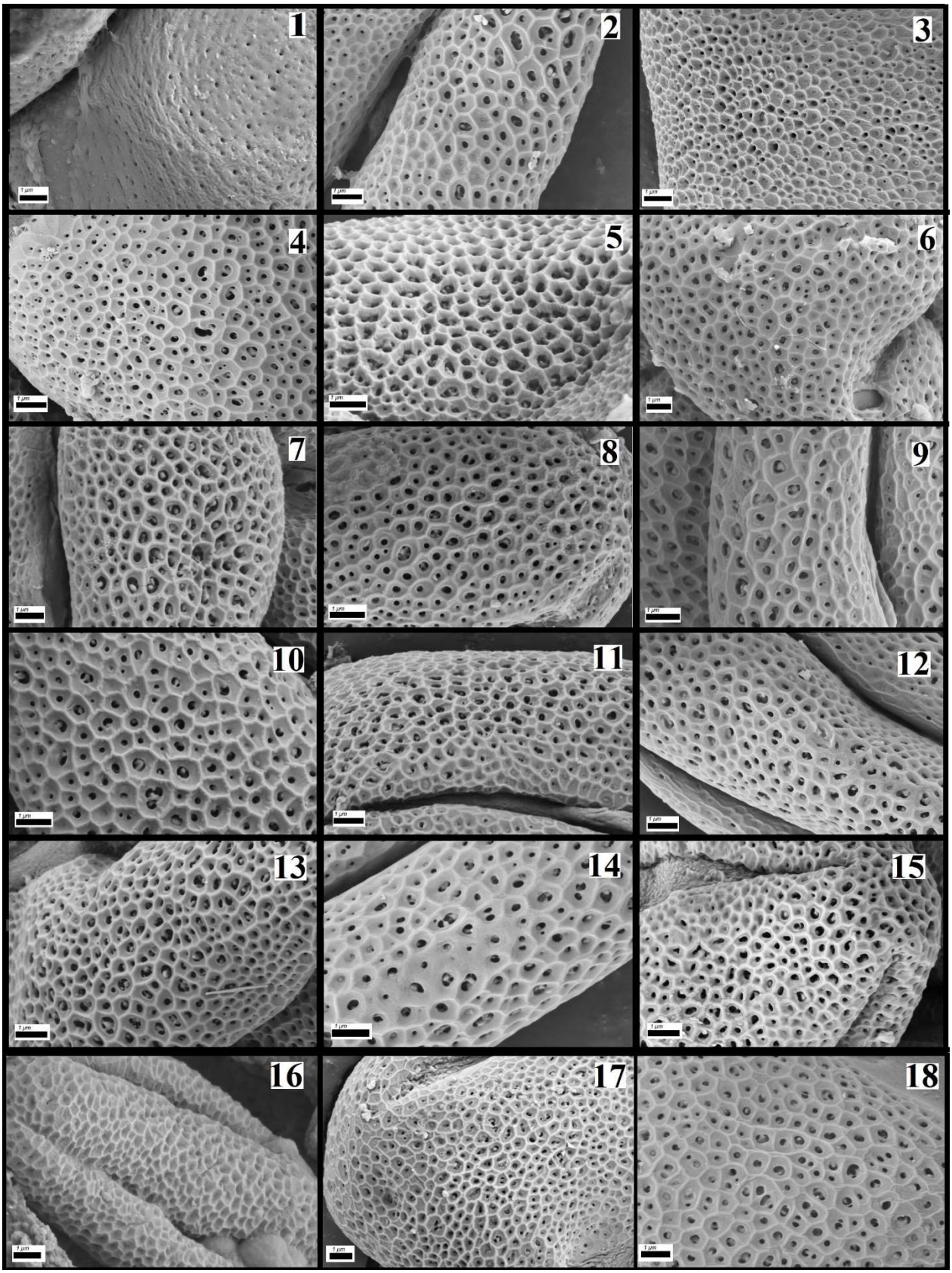


Fig. 5. *Hypericum* by Scanning Electron Microscopy (Apertural view): **1a-b.** *H. hircinum*, **2a-b.** *H. spectabile*, **3a-b.** *H. lysimachioides* var. *lysimachioides*, **4a-b.** *H. lysimachioides* var. *spathulatum*, **5a-b.** *H. elongatum* var. *elongatum*, **6a-b.** *H. elongatum* var. *antasiaticum*, **7a-b.** *H. karjaginii*, **8a-b.** *H. microcalycinum*, **9a-b.** *H. sorgerae*, **10a-b.** *H. davisii*, **11a-b.** *H. lydium*, **12a-b.** *H. pseudolaeve*, **13a-b.** *H. helianthemoides*, **14a-b.** *H. thymbrifolium*, **15a-b.** *H. uniglandulosum*, **16a-b.** *H. ekerii.* **17a-b.** *H. scabroides*, **18a-b.** *H. scabrum,* **19a-b.** *H. thymopsis*, **20a-b.** *H. confertum* subsp. *stenobotrys*, **21a-b.** *H. venustum*, **22a-b.** *H. linarioides* subsp. *linarioides* **23a-b.** *H. armenum* subsp. *armenum* **24a-b.** *H. montbretii,* **25a-b.** *H. bithynicum,* **26a-b.** *H. orientale,* **27a-b.** *H. origanifolium,* **28a-b.** *H. tetrapterum* var. *tetrapterum,* **29a-b.** *H. perforatum* subsp. *perforatum,* **30a-b.** *H. triquetrifolium* **(scale bar 3 μm)**.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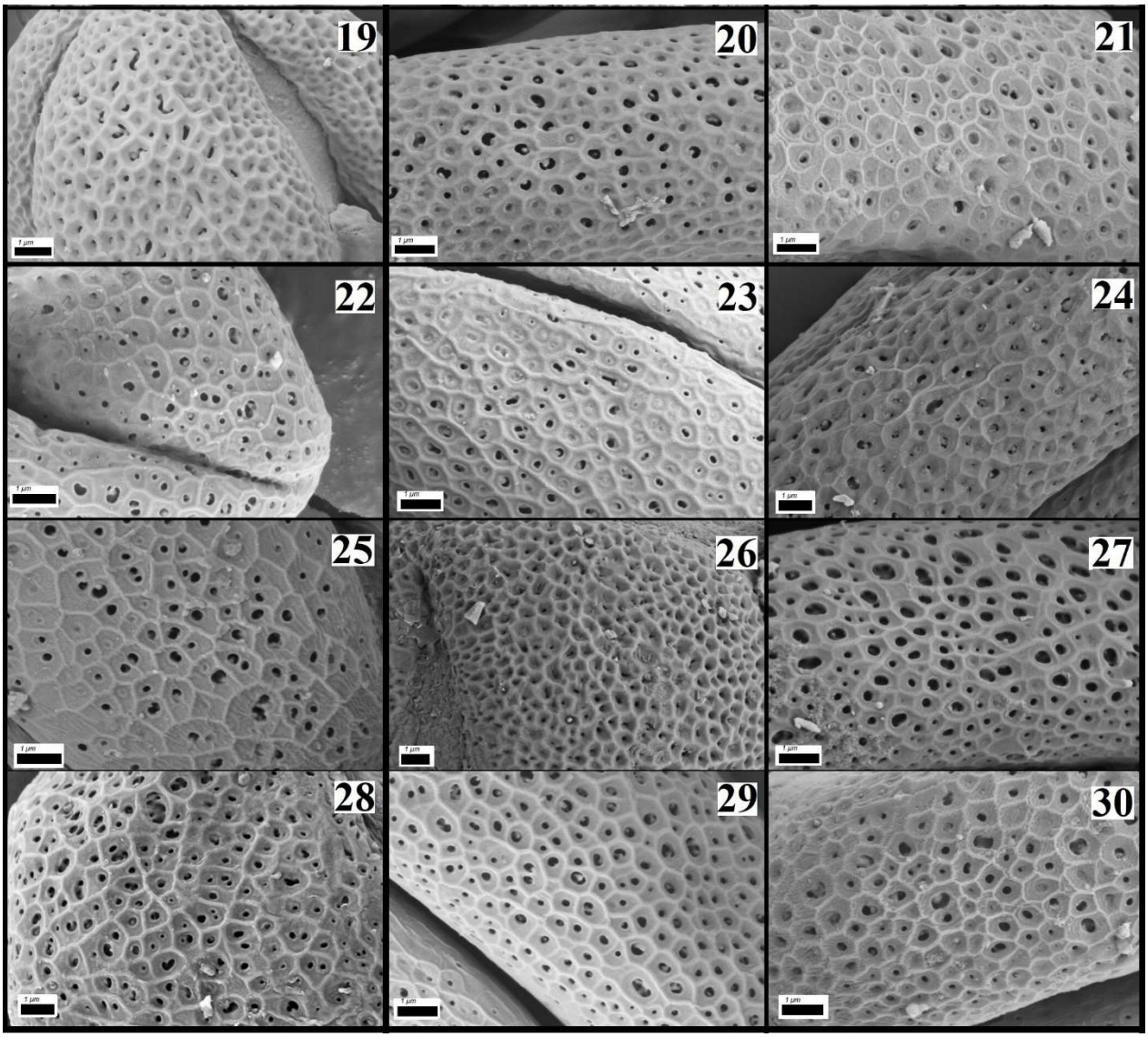

Fig. 6. *Hypericum* by Scanning Electron Microscopy (Ornamentation): **1.** *H. hircinum*, **2.** *H. spectabile*, **3.** *H. lysimachiodes* var. *lysimachiodes*, **4.** *H. lysimachiodes* var. *spathulatum*, **5.** *H. elongatum* var. *elongatum*, **6.** *H. elongatum* var. *antasiaticum*, **7.** *H. karjaginii*, **8.** *H. microcalycinum*, **9.** *H. sorgerae*, **10.** *H. davisii*, **11.** *H. lydium*, **12.** *H. pseudolaeve*, **13.** *H. helianthemoides*, **14.** *H. thymbrifolium*, **15.** *H. uniglandulosum*: **16.** *H. uniglandulosum*, **17.** *H. scabroides*, **18.** *H. scabrum,* **19.** *H. thymopsis*, **20.** *H. confertum* subsp. *stenobotrys*, **21.** *H. venustum*, **22.** *H. linarioides* subsp. *linarioides* **23.** *H. armenum* subsp. *armenum* **24.** *H. montbretii,* **25.** *H. bithynicum,* **26.** *H. orientale,* **27.** *H. origanifolium,* **28.** *H. tetrapterum* var. *tetrapterum,* **29.** *H. perforatum* subsp. *perforatum,* **30.** *H. triquetrifolium* **(scale bar 1 µm)**.

DISCUSSION

The findings from pollen morphologies of 30 taxa of the genus *Hypericum* showed that the pollen of the *Hypericum* taxa has a variety of apertures and shapes. The majority of *Hypericum* species have been discovered to have 3-colp(or)ate apertures, however, some of the investigated taxa have pollen that is syncolpo(ra)te or pantocolpo(ra)te in our study. Previous studies showed tricolporate pollen is the primary pollen type in the Hypericaceae/Guttiferae (Clarke, 1975). Additionally, Nnamani and Nwosu, (2012) found that in addition to tricolporate, Clusiaceae also has tetracolporate and zonocolporate apertural forms. In addition, Alanbari et al., (2023) found that *Hypericum* species have tricolporate except for *H. davisii,* has tetracolpate apertures. However, our study showed that *H. davisii* has 4-colpate, 6-pantocolporate, 4-syncolp(or)ate pollen apertures. Also, prolate-spheroidal pollen shapes were found to be more common rather than others in our study. The oblate-spheroidal pollen shape was only seen in *H. scabrum* and *H. hircinum*. However, *H. scabrum* had regular and irregular pollen grains, while *H. hircinum* had only regular pollen grains. Also, our study showed that the

pollen shapes of the two varieties of *H. lysimachiodes* were distinct*; H. lysimachiodes* var. *lysimachiodes* had subprolate pollen, while *H. lysimachiodes* var. *spathulatum* had spheroidal pollen, but the two subspecies aforementioned had regular and irregular pollen grains.

As shown in Table 4, pollen morphology serves as a distinguishing feature among the species within each section. In all taxa across these sections, the pollen is generally regular and isopolar. However, in the Hirtella and Hypericum sections, the pollen was observed to range from regular to irregular in shape, and polarity varied from isopolar to heteropolar. In terms of pore shape, the Androsaemum, Hirtella, Taeniocarpium, Origanifolia, and Hypericum sections exhibited lalongate pollen. The Drosocarpium and Crossophyllum sections showed exclusively lolongate pollen. Additionally, the Hirtella and Taeniocarpium sections demonstrated a broader range of forms, including lalongate, lolongate, and circular pollen shapes. All sections exhibited 3-colporate pollen apertures. Furthermore, irregular aperture types—specifically syncolporate and pantocolporate—were identified in the Hirtella and Hypericum sections. Regarding exine ornamentation, the Crossophyllum section displayed solely microreticulate patterns, whereas all other sections exhibited a combination of microreticulate and perforate ornamentation.

Our study confirmed that *Hypericum* taxa significantly vary in the number and types of apertures and pollen shapes. The number and types of apertures were noted to vary in various investigations, and pollen grains of *Hypericum* were 3-zonocolporate with a microreticulate to reticulate ornamentation pattern (Robson, 1958; Erdtman *et al.,* 1961; Clarke, 1975, 1981; Otaghvari *et al.,* 2015). Furthermore, Ocak *et al.,* (2013) discovered that the regular pollen grains of all 16 *Hypericum* taxa from Turkey are 3-zonocolporate and ornamented with microreticulate, supporting the findings of Martonfi *et al.,* (2002) that the regular pollen grains of all seven *Hypericum* species are 3-zonocolporate and can be classified as *H. perforatum* type. Martonfi *et al.,*'s, (2002) findings did not agree with our findings because *H. perforatum* subsp. *perforatum* had colporate or syncolpate pollen grains and regular and irregular pollen grains in our investigation. However, our study found that taxa with regular pollen have only 4-colp(or)ate and 3-colp(or)ate pollen. Our study also showed that *H. helianthemoides* and *H. karjaginii* only had irregular pollen grains, while some of the studied taxa had regular and irregular or regular pollen grains. According to Clarke, (1975, 1981), the pollen morphology of *Hypericum* exhibits great variation, and the genus has a variety of irregular pollen grains. These characteristics have been regarded as diagnostic evidence and useful for differentiating between species and subspecies (Otaghvari *et al.,* 2015; Faghir *et al.,* 2018). The current study's findings further showed that ornamentations with reticulate or reticulate-perforate and microreticulate or microreticulate-perforate patterns were exine sculpturing patterns of the *Hypericum* taxa under investigation. Ocak *et al.,* (2013), Faghir *et al.,* (2018), and Ozbek (*et al.,* 2019) showed that exine structure is microreticulate in *Hypericum* pollen. However, fovealote and scabrate sculptural patterns have been reported by Clarke, (1981) and Mazari *et al.,* (2017). The exine ornamentation is the key distinguishing feature for species identification and the type of pollen shape (Meseguer and Sanmartin, 2012; Otaghvari *et al.,* 2015; Faghir *et al.,* 2018). The main diagnostic characteristics are the shape of pollen grains (based on the ratio of the polar axis to equatorial diameter), type of endoaperture, and ornamentation of exine (Clarke, 1975).

The current investigation found that the colpus is narrow (1.53-5.87 µm), short to slightly long (12.17-21.33 µm), with sharp ends and distinct edges. Ocak *et al.,* (2013) also reported that the colpus length was between 11.20 µm-19.25 µm while the colpus width was between 2.70 µm and 4.40 µm. Our study also revealed that the pollen grains are small to medium-sized. In addition, it was proven that the pollen grains ranged in size from small to medium by Otaghvari *et al.,* (2015) and Faghir *et al.,* (2018). It has been suggested that the ploidy level of the species and hybridization in the genus *Hypericum* affected pollen size (Faghir *et al.,* 2018). However, according to Martonfi *et al.,* (2002), pollen size and chromosomal number have a weak correlation. For example, *H. perforatum* had triploid, tetraploid, or hexaploid chromosome numbers (Robson and Adams, 1968; Mehravi *et al.,* 2022), and *H. hircinum* had tetraploid (Butiuc-Keul *et al.,* 2022), but both species mentioned have small pollen sizes in our study. Additionally, the colpus membrane was discovered to be psilate, the form of the porus was determined to be lolongate, circular, or lalongate, and the operculum was present in all of the taxa that were examined for this study. Previous studies showed that *Hypericum* had lolongate (Clarke, 1981; Yuce Babacan *et al.,* 2017; Ozbek *et al.,* 2019), and lalongate porus (Clarke, 1981; Ozbek *et al.,* 2019), while the edge of the colpus is psilate (Faghir *et al.,* 2018) or psilate-perforate, and the operculum are present in some species (Faghir *et al.,* 2018).

On the other hand, the pollen morphological features that were measured in this study were used in cluster analysis to evaluate the *Hypericum* taxa. The results are shown in a dendrogram (Fig. 2). The UPGMA dendrogram classifies taxa into four separate groups as types 1-4 based on UPGMA results. Nürk *et al.,* (2013) also found that *H. perforatum* subsp. *perforatum, H. triquetrifolium,* and *H. tetrapterum* were clustered based on ITS sequence data, as in the results of the current study. Similarly, these three species are closely clustered. The results of the RFLP analysis of CpDNA by Pilepic *et al.,* (2010) and based on morphological features by Bi *et al.,* (2021) also showed

that these three taxa clustered together. However, *H. triquetrifolium* is put in a distinct cluster in the RAPD analysis of Bi *et al.,* (2021). Furthermore, an electrophoretic study of *Hypericum* performed by Mahditabar-Bahnamiri *et al.,* (2020) revealed that *H. perforatum* and *H. tetrapterum* were closely related. However, Kakouri et al., (2023) discovered that the chemical compositions of *H. perforatum* and *H. tetrapterum* were not the same. Additionally, according to the PCA results based on pollen morphological features, the colpus length (Clg) and mesocolpia (L) significantly influence the classification of type 1, type 2, and type 3. In the placement of type 4, the polar axis (P) and equatorial diameter (E) play opposing roles. In other words, type 4 pollen grains are smaller in size.

CONCLUSION

This study suggested that the analyzed *Hypericum* taxa had regular and irregular pollen morphologies and showed that the pollen grains of *Hypericum* taxa were diverse in size and shape. This study also discovered that most *Hypericum* taxa exhibit 3-colporate or 3-colpate apertures, and exine sculpturing patterns were microreticulate-perforate. This study also found that the investigated taxa had an operculum and that the colpus membrane was psilate, with the shape of the porus being lolongate, circular, or lalongate. The present study showed that pollen size weakly correlates with chromosome number in the literature. Additionally, our investigation revealed that *H. helianthemoides* and *H. karjaginii* only produced irregular pollen grains, in contrast to other taxa that were examined, which produced both irregular and regular or regular pollen grains. A cluster analysis was performed to assess the *Hypericum* taxa using the pollen morphological characteristics, and the taxa were split into four unique groups known as types 1-4 based on the UPGMA results. Moreover, colpus length (Clg), mesocolpia (L), polar axis (P), and equatorial diameter (E) were shown to have a significant influence on the classification of *Hypericum* taxa. According to the study's findings, the morphological characteristics of pollen can be used to help identify a genus.

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