Palynological Study of Polypodiaceae Plants in Shandong and Its Taxonomic Significance: Post-print

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Date: 2020-04-03T00:00:00+00:00

Abstract

Based on the new international classification system for lycophytes and ferns adopted in Flora of China, the Polypodiaceae family not only encompasses more than 20 genera from the Polypodiaceae in Ching Ren-Chang' s classification system, but also includes previously independent families such as Drynariaceae and Platyceriaceae. The new classification system of Polypodiaceae comprises numerous taxa and is characterized by taxonomic complexity, necessitating a re-evaluation of its rationality and the significance of palynology within this new systematic framework. For the first time employing the new classification system, this study systematically investigated the spore morphology and submicroscopic structure of perine ornamentation of Polypodiaceae species distributed in Shandong using scanning electron microscopy. The spores of this family exhibit a rounded-reniform shape with bilateral symmetry and possess a perine; the perine ornamentation demonstrates stability at the species level while showing significant differentiation among subfamilies, genera, and species. Palynological findings support the recognition of Drynarioideae and Platycerioideae as two distinct subfamilies within Polypodiaceae; based on the perine ornamentation of Phymatopteris shandongensis spores, in conjunction with leaf morphological characteristics, Phymatopteris shandongensis J. X. Li et C. Y. Wang should be recognized as an independent new species rather than being merged with Phymatopteris hastata (Thunb.) Pic. Serm. In accordance with the International Code of Nomenclature for algae, fungi, and plants and the Flora of China classification system, Phymatopteris shandongensis (J. X. Li et C. Y. Wang) is herein newly combined as Selliguea shandongensis (J. X. Li et C. Y. Wang) J. X. Li & X. J. Li, comb. nov. This study not only provides novel palynological data for Polypodiaceae for the first time, but also furnishes palynological evidence supporting its new classification system, which is concordant with DNA-based classification systems, thereby demonstrating the rationality and scientific validity of the new classification system and holding significant

importance for constructing a natural classification system for Polypodiaceae and its subfamilies.

Full Text

Palynology of the Polypodiaceae from Shandong and its Significance in Classification

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Abstract: The new classification system for lycophytes and ferns adopted in *Flora of China* incorporates an international classification framework. In this system, Polypodiaceae encompasses not only the 20+ genera of Polypodiaceae in the Qin Renchang classification system but also previously independent families such as Drynariaceae and Platyceriaceae. This new classification system for Polypodiaceae contains numerous taxa and involves complex taxonomic arrangements, necessitating fresh investigation into its rationality and the significance of palynology within this revised framework. For the first time based on the new classification system, this study systematically examines the spore morphology and submicroscopic structure of perispore ornamentation in Polypodiaceae species distributed in Shandong using scanning electron microscopy. The spores of this family are reniform, bilaterally symmetrical, and possess a perispore. The perispore ornamentation is stable within species but shows significant distinctions among subfamilies, genera, and species. Palynological findings support the placement of Drynarioideae and Platycerioideae as two distinct subfamilies within Polypodiaceae. Based on the perispore ornamentation of *Phymatopteris shandongensis* in combination with leaf morphological characteristics, *Phymatopteris shandongensis* J. X. Li et C. Y. Wang should be recognized as an independent new species rather than merged with *P. hastata* (Thunb.) Pic. Serm. In accordance with the *International Code of Nomenclature for algae, fungi, and plants* and the *Flora of China* classification system, *Phymatopteris shandongensis* (J. X. Li et C. Y. Wang) J. X. Li & C. Y. Wang is herein recombined as *Selliguea shandongensis* (J. X. Li et C. Y. Wang) J. X. Li & X. J. Li, comb. nov. This study not only provides new palynological data for Polypodiaceae but also furnishes palynological evidence for the new classification system, which aligns with DNA-based classification systems and demonstrates the rationality and scientific validity of the new framework, thereby holding significant importance for constructing a natural classification system for Polypodiaceae and its subfamilies.

Keywords: Polypodiaceae, Drynarioideae, Platycerioideae, Microsoroideae, *Selliguea shandongensis*, palynology, SEM, Shandong

Funding: This work was supported by the "National Traditional Chinese Medicine Resources Survey Project" for TCM Public Health Service Special

Subsidy in 2019 (Finance and Society [2019] No. 39).

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Academician Qin Renchang conducted extensive research on Chinese ferns, establishing the Qin Renchang classification system (Qin, 1978) and publishing *Flora Reipublicae Popularis Sinicae* 6(2) in 2000 based on this framework. In this system, Polypodiaceae (with over 20 genera), Drynariaceae, and Platyceriaceae were treated as independent families. Numerous scholars have conducted research from taxonomic (Li, 1984, 1985, 1990; Li et al., 1996; Zhang, 2012) and palynological perspectives (Zhang et al., 1976; Zhang, 1979; Zhang & Wang, 1988; Li et al., 1988; Li et al., 1997; Liu & Zhao, 1999; Li et al., 2008; Shao et al., 2010; Wang & Dai, 2010; Jiang et al., 2010; Li et al., 2016).

From the late 20th to early 21st century, the emergence of molecular biology internationally has transformed our understanding of evolutionary relationships across vascular plants. With the advent of DNA-based systematics and accumulating molecular evidence, a comprehensive familial and generic classification for lycophytes and ferns parallel to the APG system was formally proposed (Christenhusz et al., 2011) and gained widespread international recognition. Based on this new understanding, *Flora of China* (Zhang et al., 2013) and Zhang Xianchun' s classification system (Zhang & Sun, 2015) were the first in China to adopt this new framework for classifying Chinese lycophytes and ferns, updating the Qin Renchang system (Qin, 1978) and earning high recognition among Chinese pteridologists.

The new classification system for Polypodiaceae (Zhang et al., 2013; Zhang & Sun, 2015) encompasses the Polypodiaceae, Drynariaceae, Platyceriaceae, and *Microsorum* from the Qin Renchang system, reorganizing them into five subfamilies: Loxogrammoideae H. Schneid., Drynarioideae Crabbe, Jermy & Mickel, Platycerioideae B. K. Nayar, Microsoroideae B. K. Nayar, and Polypodioideae B. K. Nayar (Zhang et al., 2013; Zhang & Sun, 2015). Consequently, although both the *Flora of China*/Zhang Xianchun system (2015) and the Qin Renchang system (1978) use the same family name Polypodiaceae, the taxa included differ substantially. For the first time, we employed scanning electron microscopy to systematically observe the submicroscopic structure of spores from three subfamilies (Drynarioideae, Platycerioideae, and Microsoroideae), four genera, and nine species of Polypodiaceae distributed in Shandong, including both taxa recorded in *Flora of China* (Zhang et al., 2013) and unrecorded species (Li, 1984). This investigation aims to explore the relationship between palynology and DNA-based classification systems, evaluate the rationality of *Flora of China* (Zhang et al., 2013) and Zhang Xianchun' s system (Zhang & Sun, 2015), and provide

palynological scientific evidence for constructing a natural classification system for Polypodiaceae.

Materials and Methods

Experimental materials comprised well-developed mature spores from nine species across three subfamilies of Polypodiaceae distributed in Shandong: Drynarioideae Crabbe, Jermy & Mickel (including *Drynaria* (Bory) J. Sm. and *Selliguea* Bory), Platycerioideae B. K. Nayar (*Pyrrosia* Mirbel), and Microsoroideae B. K. Nayar [*Lepisorus* (J. Sm.) Ching] (Table 1). Voucher specimens and type specimens of the new species (Li, 1984) were identified by Li Jianxiu from Shandong University of Traditional Chinese Medicine and deposited in the Medicinal Plant Herbarium of Shandong University of Traditional Chinese Medicine (SDCM). Taxonomic names follow *Flora of China*; for the new species *Selliguea shandongensis* (J. X. Li et C. Y. Wang) J. X. Li & X. J. Li not recorded in *Flora of China*, the name published in *Acta Phytotaxonomica Sinica* (Li, 1984) based on the type specimen (J. X. Li-0109 typus) was adopted. Spore morphological characteristics were described according to palynological concepts.

1.2 Methods Mature spores were collected from voucher or type specimens of nine Polypodiaceae species distributed in Shandong. Spores were evenly dispersed on double-sided adhesive tape attached to specimen stubs, sputter-coated with gold for 2 minutes using a British SC7620 sputter coater, and then examined under a German Zeiss SUPRA™55 thermal field emission scanning electron microscope. Ten spores each were observed in polar and equatorial views. Representative spores were photographed at magnifications ranging from high power (×5,000) to low power (×1,500) after voltage stabilization and focal adjustment, with plates prepared accordingly.

Results and Analysis

The study examined well-developed mature spores from nine species across four genera and three subfamilies of Polypodiaceae distributed in Shandong: Drynarioideae Crabbe, Jermy & Mickel [*Drynaria* (Bory) J. Sm. *D. roosii* Nakaike and *Selliguea* Bory *S. hastata* (Thunb.) Fraser-Jenk., *S. shandongensis* (J. X. Li et C. Y. Wang) J. X. Li & X. J. Li]; Platycerioideae B. K. Nayar [*Pyrrosia* Mirbel *P. petiolosa* (Christ) Ching, *P. davidii* (Giesenh. ex Diels) Ching]; and Microsoroideae B. K. Nayar [*Lepisorus* (J. Sm.) Ching *L. marginatus* Ching, *L. ussuriensis* (Regel & Maack) Ching, *L. ussuriensis* var. *distans* (Makino) Tagawa, *L. thunbergianus* (Kaulf.) Ching].

All species shared common spore morphological features: polar view circular

or reniform, equatorial view circular or super-semicircular, bilaterally symmetrical, monolete with a laesura approximately 2/3 the length of the polar axis, and possessing a perispore. However, submicroscopic structures of the perispore ornamentation differed distinctly among subfamilies: Drynarioideae exhibited granular or echinate ornamentation; Platycerioideae showed tuberculate ornamentation; and Microsoroideae displayed undulate and tuberculate-rugulate ornamentation. These characteristics were stable within subfamilies, genera, and species, while showing significant differences among subfamilies, genera, and species (Table 2 , Plate I, Key).

Table 2 Spore morphology and perispore ornamentation of Polypodiaceae in Shandong

Species	Ornamentation type	Polar view	Equatorial view (m²)	Plate
Drynaria roosii Nakaike	Granulate	Circular	35.3 × 56.6	Plate I
Selliguea hastata (Thunb.) Fraser-Jenk.	Echinate	Circular	28.1 × 42.6	Plate I
Selliguea shandongensis (J. X. Li et C. Y. Wang) J. X. Li & X. J. Li	Granulate	Circular	47.0 × 52.4	Plate I
Lepisorus marginatus Ching	Sinuate	Reniform	40.6 × 58.9	Plate I
Lepisorus ussuriensis (Regel & Maack) Ching	Undulate	Reniform	37.0 × 56.6	Plate I

Species	Ornamentation type	Polar view	Equatorial view (m^2)	Plate
Lepisorus ussuriensis var. *distans* (Makino) Tagawa	Densely tuberculate-rugulate	Reniform	40.6 × 58.4	Plate I
Lepisorus thunbergianus (Kaulf.) Ching	Scarcely tuberculate-rugulate	Reniform	36.1 × 64.3	Plate I
Pyrrosia petiolosa (Christ) Ching	Tuberculate	Long circular	62.1 × 70.3	Plate I
Pyrrosia davidii (Giesenh. ex Diels) Ching	Uneven tuberculate	Circular	50.6 × 58.6	Plate I

Plate I Spore morphology of Polypodiaceae under SEM

Note: 1-4. Drynaria roosii*; 5-8.* Selliguea hastata*; 9-12.* Selliguea shandongensis*; 13-16.* Lepisorus marginatus*; 17-20.* Lepisorus ussuriensis*; 21-24.* Lepisorus ussuriensis* var. *distans*; 25-28. *Lepisorus thunbergianus*; 29-32. *Pyrrosia petiolosa*; 33-35. *Pyrrosia davidii*. 2, 6, 10, 14, 18, 22, 26, 30, 35. Local magnification of spore polar view; 4, 8, 12, 16, 20, 24, 28, 32. Local magnification of spore equatorial view.*

Key to Subfamilies, Genera, and Species

1a. Plants with humus-collecting leaves or leaf bases expanded into broad auricles for humus accumulation; perispore ornamentation granular.

2a. Humus-collecting leaves scaly, or only leaf bases expanded into broad auricles for humus accumulation; normal leaves deeply pinnatifid or pinnate; sori borne at vein forks or between two veins; without paraphyses; perispore granular ornamentation dense but unevenly distributed → **1. Drynarioideae** *Drynaria D. roosii*

2b. Humus-collecting leaves circular; normal leaves palmately dichotomously deeply lobed, antler-shaped, stellate-pubescent; sori borne at lobe forks or on

fertile frond lobes; with stellate paraphyses; perispore with sparse fine granular ornamentation → **2. Platycerioideae** *Platycerium P. wallichii*

1b. Plants without humus-collecting leaves or expanded leaf bases for humus accumulation; perispore ornamentation tuberculate, echinate, fine granular, undulate, or tuberculate-rugulate.

3a. Sori small, multiple rows on abaxial leaf surface, covered by stellate hairs, with stellate paraphyses; perispore ornamentation tuberculate → **2. Platycerioideae** *Pyrrosia*

4a. Leaves monomorphic, narrowly lanceolate, apex acuminate; perispore with uneven tuberculate ornamentation → *P. davidii*

4b. Leaves sub-dimorphic, narrowly lanceolate, apex obtuse; perispore with even tuberculate ornamentation → *P. petiolosa*

3b. Sori large, circular, dorsal on both sides of main leaf vein, without stellate hairs.

5a. Leaves simple, undivided, or deeply pinnatifid or pinnate, without paraphyses; perispore ornamentation echinate or fine granular → **1. Drynarioideae** *Selliguea*

6a. Leaves deeply pinnatifid or pinnate; perispore with echinate ornamentation → *S. hastata*

6b. Leaves simple, undivided; perispore with fine granular ornamentation → *S. shandongensis*

5b. Leaves simple, undivided, linear or lanceolate, with paraphyses; perispore ornamentation undulate or tuberculate-rugulate → **3. Microsoroideae** *Lepisorus*

7a. Rhizome scales with transparent mesh.

8a. Rhizome scales sub-ovate, with fine transparent mesh; leaf width usually 2–3 cm, with cartilaginous narrow margin; perispore with deep undulate ornamentation → *L. marginatus*

8b. Rhizome scales ovate-lanceolate or triangular-ovate, with coarse mesh.

9a. Rhizome scales ovate-lanceolate, with large transparent mesh; leaves linear-lanceolate, middle width 0.5–1 cm, apex shortly acuminate; perispore with undulate ornamentation → *L. ussuriensis*

9b. Rhizome scales triangular-ovate, with large transparent mesh; leaves lanceolate, apex acuminate; perispore with densely tuberculate-rugulate ornamentation → *L. ussuriensis* var. *distans*

7b. Rhizome scales lanceolate, with fine mesh, mesh opaque, only 1–2 rows of marginal mesh transparent; leaves linear-lanceolate, apex acuminate; perispore with scarcely tuberculate-rugulate ornamentation → *L. thunbergianus*

3.1 Significance of Palynology in the Polypodiaceae Classification System

The new classification system for Polypodiaceae examined in this study refers to the revised concept of Polypodiaceae in *Flora of China* (Zhang et al., 2013) and Zhang Xianchun' s system (Zhang & Sun, 2015). Although both this system and the plant taxonomy-based Qin Renchang system (Qin, 1978) employ the same family name Polypodiaceae, the taxa encompassed differ substantially. The latter includes only Polypodiaceae sensu stricto, comprising over 20 genera such as *Lepisorus* (J. Sm.) Ching, *Pyrrosia* Mirbel, and *Phymatopteris* Pic. Serm. In contrast, the former, based on DNA molecular systematics as implemented in *Flora of China* (Zhang et al., 2013) and Zhang Xianchun' s new system (Zhang & Sun, 2015), includes not only the Polypodiaceae of the Qin Renchang system but also several previously independent families including Drynariaceae and Platyceriaceae. Polypodiaceae is subdivided into five subfamilies: Loxogrammoideae H. Schneid. (not occurring in Shandong), Drynarioideae Crabbe, Jermy & Mickel (including *Drynaria* (Bory) J. Sm. and *Selliguea* Bory [Phymatopteris Pic. Serm.]), Platycerioideae B. K. Nayar (including *Platycerium* Desv. and *Pyrrosia* Mirbel), Microsoroideae B. K. Nayar [*Lepisorus* (J. Sm.) Ching], and Polypodioideae B. K. Nayar (not occurring in Shandong).

Spores represent the core reproductive organ of ferns, serving as the primary site for genetic material and expressing highly stable morphological characteristics. Spore morphology holds significant importance in fern taxonomy and phylogenetic studies, as exine and perispore ornamentation patterns vary considerably among different taxa, serving as important features for distinguishing taxonomic groups and establishing higher-level taxonomic units (Lu et al., 2007). This study represents the first comprehensive investigation combining taxonomic, systematic, and palynological approaches to Polypodiaceae based on the new classification system of *Flora of China* (Zhang et al., 2013) and Zhang Xianchun (Zhang & Sun, 2015), with no comparable reports in domestic or international literature.

Under SEM, the bilaterally symmetrical, monolete spores with perispore and submicroscopic structural characteristics, showing polar views from circular to reniform and equatorial views from circular to super-semicircular, hold important taxonomic significance at familial and subfamilial levels. Palynological evidence aligns with DNA-based systematic classification, providing scientific support for the rationality, objectivity, and scientific validity of establishing subfamilies within Polypodiaceae and confirming its status as a major natural group. This study demonstrates that *Drynaria* (1 species), with reference to four species studied by Wang & Dai (2010), consistently exhibits granular perispore ornamentation; *Selliguea* (2 species), with reference to three species studied by Wang & Dai (2010), shows echinate and fine granular ornamentation; *Platycerium*, with reference to six species studied by Wang & Dai (2010), displays echinate and fine granular ornamentation; *Pyrrosia* (2 species) exhibits tuberculate ornamentation; and *Lepisorus* (4 species) shows undulate and tuberculate-rugulate

ornamentation, all consistent with Wang & Dai (2010). These perispore ornamentation patterns hold significant taxonomic value at the generic level, not only accumulating new palynological data for the Polypodiaceae classification system in *Flora of China* (Zhang et al., 2013) and Zhang Xianchun (Zhang & Sun, 2015), but also providing palynological evidence supporting the rationality of this new system that aligns with DNA-based classification. Furthermore, this work provides spore morphological criteria for subfamilial, generic, and closely related species identification, holding substantial significance for constructing a natural classification system for Polypodiaceae.

3.2 Significance of Perispore Ornamentation Submicroscopic Structure in Interspecific Classification

Phymatopteris shandongensis J. X. Li et C. Y. Wang, described as a new species in 1984 (Li, 1984), was recorded in *Flora of Shandong* (Li, 1990). However, *Flora Reipublicae Popularis Sinicae* 6(2) (Chinese Academy of Sciences, 2000) merged it with *Phymatopteris hastata* (Thunb.) Pic. Serm., adopting the latter name. *Flora of China* subsequently listed it as a synonym under *Selliguea hastata* (Thunb.) Fraser-Jenk. (Zhang et al., 2013). *Phymatopteris shandongensis* possesses simple leaves with elliptical blades, obtuse apices, and extremely slender petioles, with perispore exhibiting distinct fine granular ornamentation (Li et al., 2016), contrasting sharply with the echinate ornamentation of *Phymatopteris hastata* spores (Li et al., 2016). These represent two fundamentally different submicroscopic structural features of perispore ornamentation.

Certain ferns exhibit plant morphology extremely similar to related species, making classification based solely on macroscopic morphological characteristics difficult and long considered challenging by pteridologists. With scientific advancement, diversified research methods, and deeper investigation, classical taxonomy relying exclusively on macroscopic morphological features is insufficient. Integration of scanning electron microscopy with perispore submicroscopic structure analysis is necessary to resolve taxonomic challenges in certain groups. Spore ornamentation characteristics have been used to distinguish closely related species within *Phymatopteris* (Shao et al., 2010). Based on this significant difference in perispore ornamentation, combined with other leaf characteristics of *P. shandongensis*, we cannot accept the treatment in *Flora Reipublicae Popularis Sinicae* 6(2) (Chinese Academy of Sciences, 2000) and *Flora of China* (Zhang et al., 2013). We previously published recommendations to restore *Phymatopteris shandongensis* J. X. Li et C. Y. Wang to species status and validate its taxonomic position (Li et al., 2016). In accordance with the *Selliguea* Bory classification system in *Flora of China* and relevant provisions of the *International Code of Nomenclature*, we herein propose the new combination *Selliguea shandongensis* (J. X. Li et C. Y. Wang) J. X. Li & X. J. Li, comb. nov.

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Note: Figure translations are in progress. See original paper for figures.