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Micro-morphological characters in Polypodiaceae and its taxonomic significance

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Abstract. The present study insights into the interrelationships and taxonomic segregation of some Polypodiaceous fern taxa based on leaf architecture and foliar micro-morphology. Twenty-seven fern species were examined and valuable qualitative and quantitative data were obtained to generate UPGMA dendrogram. A dichotomous key differentiating the taxa was prepared. Results reveal that even though species have overlapping characters, certain specific traits prove taxonomically valuable. The results proved that traits like leaf shape, higher order leaf venation, stomatal and epidermal features are indeed important diagnostic characters and hence can be used for the identification of fern species in their immature stage or even in absence of sori. These data sets often combined with other morphological as well molecular data would contribute to fern phylogenetic study particularly of the large and complex family Polypodiaceae.

Keywords: Epidermis, ferns, leaf architecture, stomata.

INTRODUCTION

Polypodiaceae *s.l.* is an extant, monophyletic family of ferns that includes Polypodiaceae and previously segregated families Grammitidaceae and Platyceriaceae (Smith et al. 2008). As per PPGI (2016), Polypodiaceae comprise 6 sub-families, 65 genera, and 1,652 species and it is the second largest family of ferns (Hori et al. 2022). However, earlier reports estimate approximately 50 genera under the family worldwide (Tryon and Tryon 1982; Hennipman et al. 1990; Parris 1990; Smith et al. 2008). The family is a sub-cosmopolitan group mainly characterized by creeping stems covered with varying scales, fronds attached to phyllopodia, venation free or sometimes areolate with free or included veins, round to globose exindusiate, sori on abaxial lamina surface with yellowish to greenish monolete spores (Tryon and Tryon 1982; Hennipman et al. 1990; Parris 1990; Smith et al. 2008).

Kubitzki (1990) initially coined the term "polygrammoid ferns" until a phylogenetic study established the name Polypodiaceae (Schneider et al. 2004). Phylogenetic studies of major derived fern groups, such as asplenioid, dryopteroid, and polygrammoid ferns, have been of great importance since the ferns are an integral component of the tropical vegetation (Schneider et al. 2004). Major generic-level recircumscriptions have been suggested for Polypodiaceae with a redefinition of *Polypodium* L., *Pleopeltis* Humb. & Bonpl. ex Willd. and allied genera (Smith et al. 2008). Christenhusz et al. (2011), suggested the need for more studies at the generic level, especially on relationships among genera in some of the large families including Polypodiaceae. The order Polypodiales have been segregated into three groups with Polypodiaceae included within eupolypods I (PPG I 2016). The group eupolypods I showed diverse morphological variations with species richness and limited data sets, hence the classification or identification up to generic and specific levels is often associated with difficulty (Rothfels et al. 2012; Tan and Buot 2020).

The correct identification and classification of fern is associated with complexities since the time of Linnaeus and even in the modern era. Several genera like *Loxogramme* (Blume) C.Presl lacked published generic revision and comprehensive analyses of the genus *Arthromeris* (T.Moore) J.Sm. are unavailable. *Microsorum* Link is apparently paraphyletic relative to some other species but requires further study (PPG I 2016). The concept of family is not well established due to the existence of shared morphological features between the families (Christenhusz and Chase 2014). Even with the availability of molecular data for classification and phylogeny, Takhtajan (1996), Christenhusz and Chase, (2014), and Christenhusz et al. (2015) pointed out several difficulties such as random changes in DNA sequences, convergent evolution, parallelism, splitting and lumping of huge data set.

Morphological references of medicinal fern species are of utmost importance so that the samples can be correctly identified especially when there are chances leading to confusion and improper use of those particular taxa (Oliveira et al. 2017).It seems that Pteridaceae and Polypodiaceae contribute the highest number of medicinal fern species with worldwide distribution (Muhammad et al. 2020). Some of the species investigated in our study have important medicinal aspects. The roots of *Arthromeris wallichiana* (Spreng.) Ching antiseptic properties (Manandhar 2002), and anti-dysentery (Gaur and Bhatt 1994; Nwosu 2002). Similarly, *Drynaria quercifolia* L. has wound healing properties, lumbago treatment, rhizome astringent, and against hectic fever and cough (May 1978; Gaur and Bhatt 1994). *Microsorum membranaceum* (D.Don) Ching provides relief for chest pain, cough and cold of infant, diarrhea, and dysentery (Gaur and Bhatt 1994). Leaf juice of *Microsorum punctatum* (L.) Copel. serves as a purgative, diuretic, and wound healer (May 1978). *Phymatosorus scolopendria* (Burm.f.) Pic.Serm. is used against chronic diarrhea, anti-inflammatory, pulmonary and liver disease treatment (Mannan et al. 2008; Hoet al. 2011). *Pyrrosia lanceolata* (L.) Farw. has been used to treat skin disorders, colds, and sore throats (Benjamin and Manickam 2007).

Leaves have significance in evolutionary and developmental studies, because they are the most conspicuous organs of the plants. The leaves or fronds of ferns display great morphological diversity (Creese et al. 2010; Vasco et al. 2013). Systematists overlook the importance of vegetative characters such as leaf venations because of the perception that they are phenotypically plastic characters (Larano and Buot 2010).

However, over the years numerous species of angiosperms have been identified, described and delineated, generating phylogenetic relationships using leaf architecture Cervantes et al. 2009; Pacheco-Trejo et al. 2009; Sarala and Vijay 2014; Sharma et al. 2016; Fayed et al. 2020). Foliar micro-morphological traits like epidermal cell size, stomatal features, and laminar indument have great taxonomic implications in distinguishing species (Baronova 1992; Chukwuma et al. 2017; Chukwuma et al. 2022).

Most studies reveal that leaf venation was genetically fixed and closely related to the development and their evolution (Roth-Nebelsick et al. 2001). Therefore, it can be utilised by systematics, especially for plants without reproductive parts (Carlquist 1961; Dilcher 1974). Recent studies have further associated the lamina shape and petiole structure with plant carbon budget (Takenaka 1994; Semchenko and Zobel 2007; Niinemets et al. 2007). Description and characterization of the families under eupolypods I have included leaf dissection and venation (Pray 1960; Wagner 1979; Pryer et al. 1995; Ding et al. 2014). Some of the earlier works on leaf architecture of ferns included *Diplazium* Sw. species (Conda et al. 2017), *Lygodium* Sw. (Shinta et al. 2012), *Ophioglossum* L. (Magrini and Scoppola, 2010), and some terrestrial and epiphytic eupolypod ferns (Tan and Buot 2019) from Araucaria forest (Larcher et al. 2013).

Exploration of leaf architectural characters in selected eupolypods I group exhibited higher degree of venations until areoles only in some species under Polypodiaceae and Tectariaceae (Tan and Buot 2020). More studies for other species through leaf architecture are highly recommended to strengthen its affectivity and usefulness (Conda et al. 2017).

Over the years, significant information on certain species within the family Polypodiaceae has been generated by several studies worldwide on morphological, molecular, ecological, and distributional aspects. However, a comparative study on the species with respect to leaf architecture and venation pattern is limited. The

Polypodiaceous ferns are exceptionally diverse and thus an ideal system for investigating taxonomic and systematics of leaf form venation, epidermal features, and their variations.

This study explores the use of leaf architecture and other details in some members of Polypodiaceae and helps in taxonomic delineation which would complement the already established diagnostic characters for identification of the taxa.

MATERIALS AND METHODS

Plant material

Fresh specimens of Polypodiaceae were used for the present study. They were collected mainly from the forests of Darjeeling Himalaya which is a part of the eastern Himalaya hotspot, extending between 27°13'10''N to 26°27'05''N and 88°53'E to 87°59'30''E and lies on the northern part of the Indian state of West Bengal. The specimens were carefully identified with the help of available literature (Mehra and Bir 1964; Ghosh et al. 2004; Fraser-Jenkins 2008; Kholia 2010; Frazer-Jenkins et al. 2021). Lloyd Botanic Garden Herbarium, Darjeeling and Calcutta University Herbarium (CUH) were also consulted for proper identification. Correct nomenclature was maintained following Smith et al. (2006), Pteridophyte Phylogeny Group (PPG I 2016), and databases like Global Biodiversity Information Facility (GBIF 2022) and World Flora Online (WFO 2022). The species were assigned with a code having three lettersto the generic and specific names (see Table 1).

Leaf morphometric and venation study

Mature leaves of the target species were collected from 3 representative plants and the samples were then washed properly. For the venation study, the method of Yu and Chen (1986) was followed with some modifications. Leaves were boiled in water for 10-20 minutes, then placed in 1-5% NaOH, the strength depending on the thickness of the material. NaOH solution was changed every 1-2 days during the clearing process, which generally took 2-10 days. For some species with thick lamina, the leaves were boiled in water before being macerated in 35% NaOCl solution. Cleared leaves were then rinsed in running water thoroughly, dried, stained in 1% safranin, and mounted on slides with glycerine.

The minor venation patterns were studied by cutting a small bit from the mid portion of the leaf skeleton. Leaves were examined and photographed under Wild M3 Heerbrugg and binocular microscope Leitz Laborlux D. The terminology of Hickey (1973), Ash et al. (1999), Ellis et al. (2009), Conda et al. (2017) and Conda and Buot (2018) have been followed for the description of the leaf architecture and venation patterns.

Leaf epidermal study

The epidermal characters were analysed using different quantitative measures *viz.*,the number of epidermal cells, epidermal cell size (L x W), stomata size (L x W), stomatal pore size (L x W), and stomatal index (SI). Epidermal cell measurements from adaxial and abaxial surfaces were determined under 40x magnification with a fitted ocular scale. The stomatal index was measured following Salisbury (1928, 1932), as $SI = S/E+S \times 100$.

Statistical analysis

All the quantitative data were subjected to descriptive statistics and analysed using PAST version 4.03 (Hammer et al. 2001) to obtain a UPGMA (Unweighted Pair Group Method with Arithmetic Mean) based dendrogram.

RESULTS

The leaf architectural characters of 27 fern species were examined based on three aspects. First, the morphological characters like lamina division, shape, apex shape, blade class, base shape, base angle, base symmetry, and margin were studied. Secondly, the leaf venation details from primary to tertiary and higher order vein categories and areoles were focused upon. The leaf epidermal cells and stomata were later analysed with the aid of microscopy.

Leaf morphological trait and venation

The species under the Polypodiaceae family exhibited variable morphological characteristics that were taxonomically significant such as the leaf organisation varying from simple to pinnate, pinnatifid, imparipinnate, etc. The leaf shape ranges from lanceolate, ovate-lanceolate, oblong, linear-lanceolate to elliptic. The blade class ranged from nanophyll to macrophyll while the margins observed were mostly entire to serrate, serrulate, crenate etc. (Table 1).

Table 1. Summary of foliar micro-characters of the studied taxa

Species	Species code	Lamina division	Shape	Apex shape	Blade class	Base shape	Base angle	Base symmetry	Margin
Arthromeris himalovata Fraser-Jenk. & Kandel	*Art him*	1-pinnate	ovate-lanceolate	caudate	notophyll	rounded	obtuse	symmetrical	entire
A. lehmannii (Mett.) Ching	*Art leh*	1-pinnate	lanceolate	acuminate	microphyll	rounded	acute	symmetrical	minutely toothed
A. wallichiana (Spreng.) Ching	*Art wal*	1-pinnate	ovate-lanceolate	acuminate	mesophyll	obliquely cordate	acute	symmetrical	entire
Drynaria propinqua (Wall. ex Mett.) J.Sm. ex Bedd.	*Dry pro*	pinnatifid	ovate-lanceolate	acute	mesophyll	adnate	obtuse	symmetrical	slightly crenate
D. quercifolia L.	*Dry que*	pinnatifid	broadly lanceolate	acute	mesophyll	adnate	obtuse	symmetrical	entire
Goniophlebium argutum (Wall. ex Hook.) J.Sm.	*Gon arg*	1-pinnate	linear lanceolate	acuminate	mesophyll	broad	obtuse	symmetrical	mucronate
Lepisorus contortus (Christ) Ching	*Lep con*	simple	linear to elliptic lanceolate	acute	microphyll	attenuate	acute	symmetrical	entire
L. loriformis (Wall. ex Mett.) Ching	*Lep lor*	simple	linear	acuminate	notophyll	decurrent	acute	symmetrical	entire
L. mehrae Fraser-Jenk.	*Lep meh*	simple	linear-lanceolate	acuminate	mesophyll	attenuate	acute	symmetrical	entire
L. normalis (D.Don) C.F.Zhao, R.Wei & X.C.Zhang	*Lep nor*	simple	lanceolate	acuminate	notophyll	attenuate	acute	symmetrical	entire
L. nudus (Hook.) Ching	*Lep nud*	simple	lanceolate	acuminate	notophyll	attenuate	acute	symmetrical	entire
L. rostratus (Bedd.) C.F.Zhao, R.Wei & X.C.Zhang	*Lep ros*	simple	elliptic	acuminate	nanophyll	attenuate	acute	symmetrical	entire
L. sublinearis (Baker ex Takeda)	*Lep sub*	simple	broadly lanceolate	acuminate	microphyll	attenuate	acute	symmetrical	entire
Loxogramme involuta (D.Don) C.Presl	*Lox inv*	simple	lanceolate	acuminate	mesophyll	attenuate	acute	symmetrical	entire
Microsorum membranaceum (D.Don) Ching	*Mic mem*	simple	lanceolate	acute	mesophyll	decurrent	obtuse	symmetrical	entire
M. punctatum (L.) Copel.	*Mic pun*	simple	linear-lanceolate	acute	mesophyll	decurrent	acute	symmetrical	entire
Phymatosorus cuspidatus (D.Don) Pic.Serm.	*Phy cus*	imparipinnate	linear-lanceolate	acuminate	microphyll	attenuate	acute	symmetrical	entire
P. scolopendria (Burm.f.) Pic.Serm.	*Phy sco*	pinnatifid	oblong	acuminate	microphyll	cuneate	obtuse	symmetrical	entire
Pichisermollodes ebenipes (Hook.) Fraser-Jenk.	*Pic ebe*	palmatifid	lanceolate	acuminate	microphyll	adnate/ deflexed	obtuse	symmetrical	slightly serrulate
P. stewartii (Bedd.) Fraser-Jenk.	*Pic ste*	pinnately parted	lanceolate	acuminate	microphyll	adnate	obtuse	symmetrical	serrulate
Polypodiodes amoena (Wall. ex Mett.) Ching	*Pol amo*	deeply pinnatifid	oblong-lanceolate	acute	microphyll	adnate	obtuse	symmetrical	serrate
Pyrrosia costata (C.Presl ex Bedd.) Tagawa & K.Iwats.	*Pyr cos*	simple	oblong-lanceolate	caudate	mesophyll	decurrent	acute	symmetrical	entire
P. heteractis (Mett. ex Kuhn) Ching	*Pyr het*	simple	ovate-lanceolate	caudate-acuminate	microphyll	round	obtuse	symmetrical	entire
P. lanceolata (L.) Farw.	*Pyr lan*	simple	narrow-lanceolate	acuminate	nanophyll	attenuate	acute	symmetrical	entire
P. mannii (Giesenh.) Ching	*Pyr man*	simple	lanceolate	acute	notophyll	attenuate	acute	symmetrical	entire
Selliguea griffithiana (Hook.) Fraser-Jenk.	*Sel gri*	simple	lanceolate	acuminate	microphyll	cuneate	acute	symmetrical	entire
S. oxyloba (Wall. ex Kunze) Fraser-Jenk.	*Sel oxy*	deeply pinnatifid	ovate	acute	microphyll	adnate	obtuse	symmetrical	entire

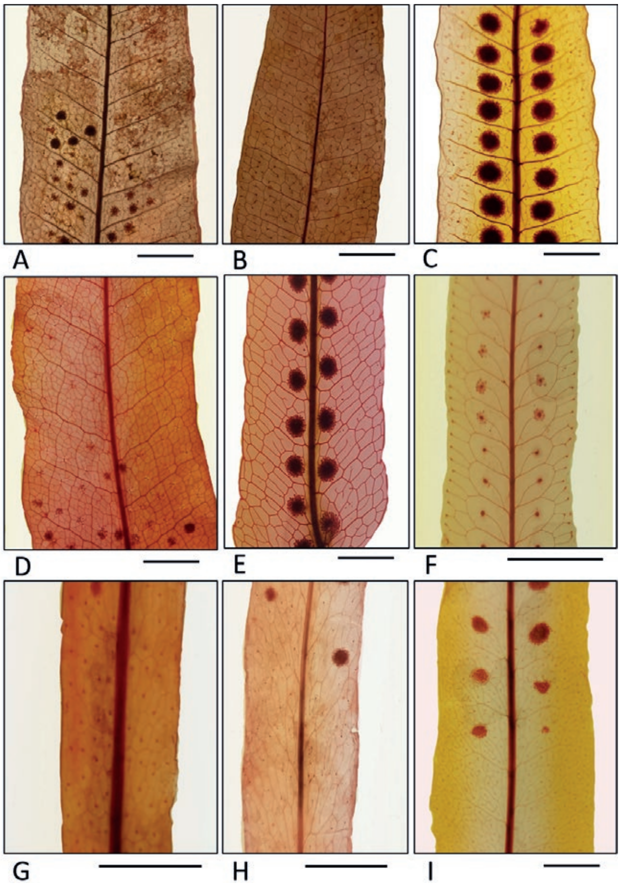

Figure 1. Photomicrographs of leaf venation in Polypodiaceae: **A**-*Arthromeris himalovata*; **B**-*Arthromeris lehmanii*; **C**-*Arthromeris wallichiana*; **D**-*Drynaria quercifolia*; **E**-*Drynaria propinqua*; **F**-*Goniophlebium argutum*; **G**-*Lepisorus contortus*; **H**-*Lepisorus loriformis*; **I**-*Lepisorus mehrae* (Scale bar-5mm).

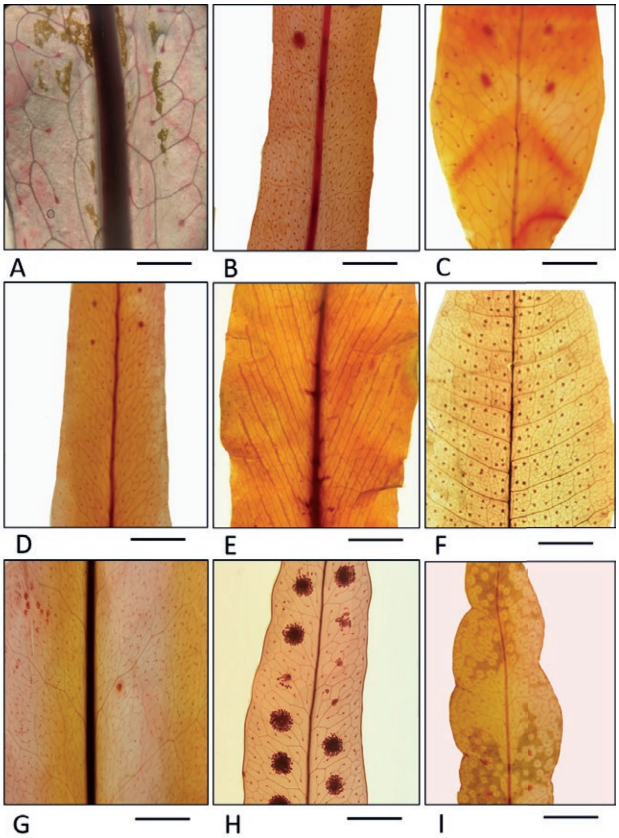

Figure 2. Photomicrographs of leaf venation in Polypodiaceae: **A**-*Lepisorus normalis;* **B**-*Lepisorus nudus*; **C**-*Lepisorus rostratus*; **D**-*Lepisorus sublinearis*; **E**-*Loxogramme involuta*; **F**-*Microsorum membranaceum*; **G**-*Microsorum punctatum*; **H**- *Phymatosorus cuspidatus*; **I**-*Phymatosorus scolopendria* (Scale bar-5mm).

The venation patterns of the species were complex which mostly ended up to 4° vein with areoles. All the species exhibited pinnate 1° vein with moderate to stout primary vein. The higher and finer secondary (2°) and tertiary (3°) venations up to quaternary (4°) vein, and areoles were also observed in most of the species (Table 2, Figures 1-3).

The marginal venation of the leaves was observed and their variation were noted which aids in the taxonomic delimitation of the species. Prominent marginal secondary veins were observed in *Arthromeris wallichiana*, *Drynaria quercifolia*, and *Drynaria propinqua*. In the species of *Lepisorus, Pyrrosia heteractis*, *Microsorum membranaceum, Phymatosorus cuspidatus* and *Phymatosorus scolopendria* the marginal veins are looped and in some taxa like *Microsorum punctatum*, *Pyrrosia costata*, *Pyrrosia mannii*, and *Pyrrosia lanceolata,* incompletely looped margins have been observed (Figures 4-6).

The areoles were mostly formed by the tertiary and quaternary veins in all the studied taxa except in *Goniophlebium argutum* and *Polypodoides amoena* where secondary veins anastomoses to form large costal areole and free forked marginal veins (Figures 1 & 3). The size of the areoles and other quantitative details of the studied taxa have been tabulated (Table 3).

Epidermal cells and stomata

Our study is focused on the mature epidermis. The epidermal cells of most of the species were irregular, with the anticlinal walls sinuous, slightly lobed in *Pyrrosia heteractis* and *Pyrrosia costata* to straight in *Pyrrosia lanceolata* and *Pyrrosia mannii*. A significant variation was observed in epidermal cell length and width among species. Mean epidermal cell length on the abaxial surface was least (26.8±0.4μm) in *Arthromeris himalovata* to (85.3±0.7μm) in *Pyrrosia costata* while mean

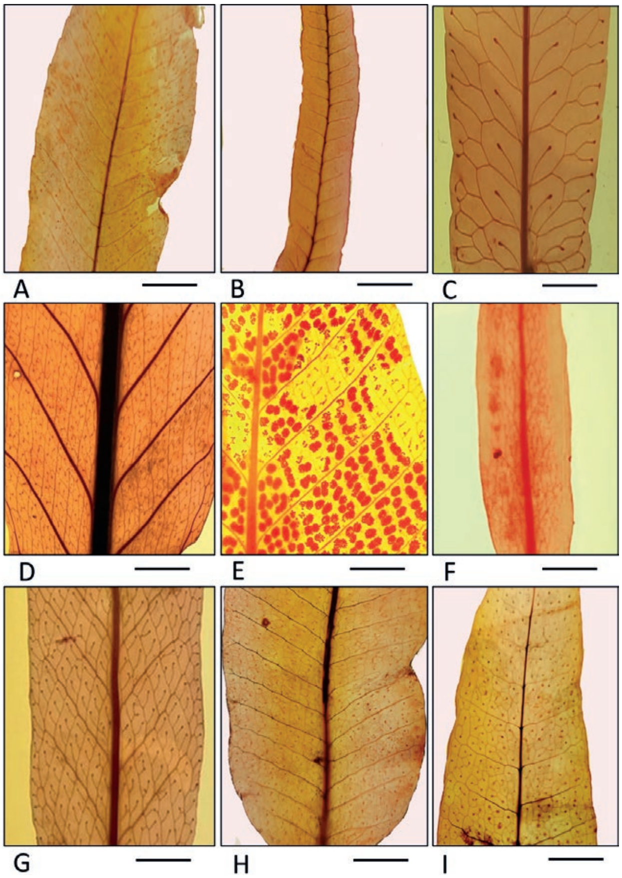

Figure 3. Photomicrographs of leaf venation in Polypodiaceae: **A**-*Pichisermollodes ebenipes;* **B**-*Pichisermollodes stewartii*; **C**-*Polypodoides amoena*; **D**-*Pyrrosia costata*; **E**-*Pyrrosia heteractis*; **F**-*Pyrrosia lanceolata*; **G**-*Pyrrosia mannii*; **H**-*Selliguea griffithiana*; **I**-*Selliguea oxyloba* (Scale bar-5mm).

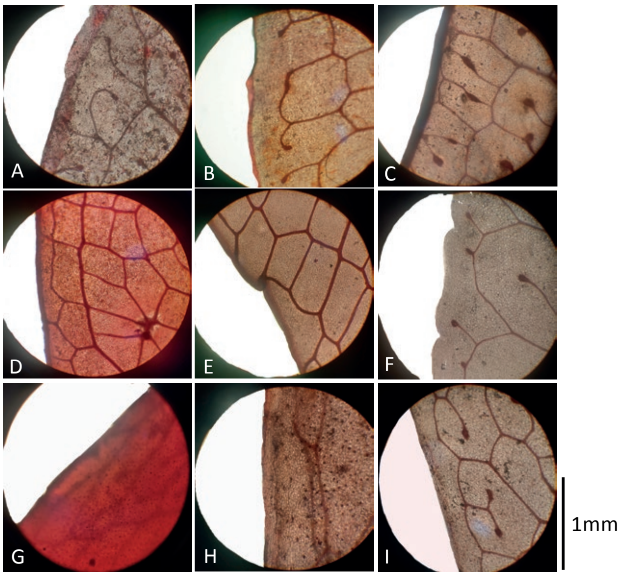

Figure 4. Photomicrographs of marginal leaf venation in Polypodiaceae: **A**-*Arthromeris himalovata*; **B**-*Arthromeris lehmanii*; **C**-*Arthromeris wallichiana*; **D**-*Drynaria quercifolia*; **E**-*Drynaria propinqua*; **F**-*Goniophlebium argutum*; **G**-*Lepisorus contortus*; **H**-*Lepisorus loriformis*; **I**-*Lepisorus mehrae.*

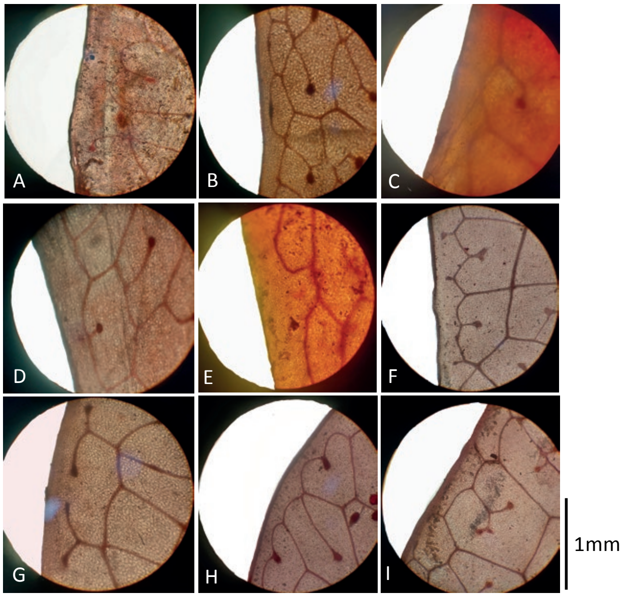

Figure 5. Photomicrographs of marginal leaf venation in Polypodiaceae: **A**-*Lepisorus normalis;* **B**-*Lepisorus nudus*; **C**-*Lepisorus rostratus*; **D**-*Lepisorus sublinearis*; **E**-*Loxogramme involuta*; **F**-*Microsorum membranaceum*; **G**-*Microsorum punctatum*; **H**-*Phymatosorus cuspidatus*; **I**-*Phymatosorus scolopendria.*

width ranged from16±0.5μm in *Arthromeris himalovata* to 55.2±0.4μm in *Lepisorus nudus*. On the abaxial side, the mean epidermal cell length was lowest (88.6±0.5μm) in *Pyrrosia costata* to highest (27.5±0.3μm) in *Arthromeris himalovata* (Table 4). Likewise, the number of lobes per cell varied from 3 to 16 among studied taxa. The minimum number of lobes per cell differed from 3 to 4 on the abaxial surface of *Lepisorus loriformis* whereas 8 to 16 on the adaxial surface of *Selliguea griffithiana*. Stomata in Polypodiaceous species under investigation are restricted to the abaxial surface of the leaf, hence they are hypostomatic. Stomatal cells have been observed all over the lamina except the vein on the abaxial surface. The stomata on a single leaf can be categorized into two or more types in all the species. The average length of stomata varied from 18.5±0.6μm in *Arthromeris himalovata* to 48.3±0.1μm in *Loxogramme involuta*, while mean stomatal width ranged from11.5±0.4μm in *Selliguea griffithiana* to 33.8±0.3μm in *Loxogramme involuta*.

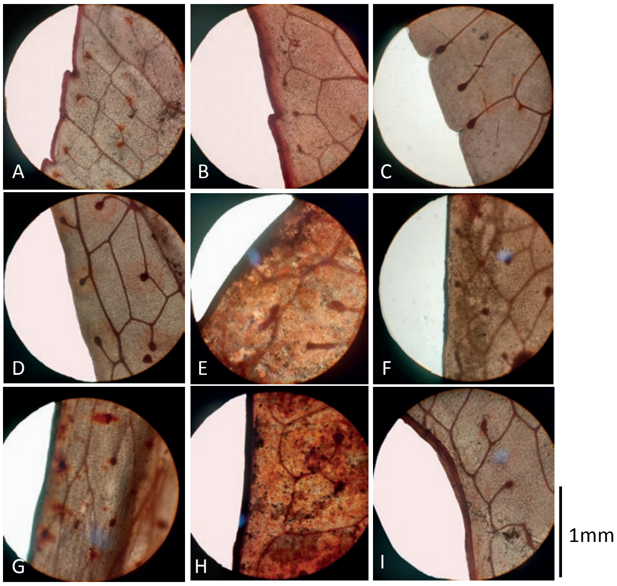

Figure 6. Photomicrographs of marginal leaf venation in Polypodiaceae: **A**-*Pichisermollodes ebenipes*; **B**-*Pichisermollodes stewartii*; **C**-*Polypodoides amoena*; **D**-*Pyrrosia costata*; **E**-*Pyrrosia heteractis*; **F**-*Pyrrosia lanceolata*; **G**-*Pyrrosia mannii*; **H**- *Selliguea griffithiana*; **I**-*Selliguea oxyloba.*

The stomatal index value ranged from 9.04±0.1 to 46.15±0.3 with the lowest in *Loxogramme involuta* followed by *Pyrrosia lanceolata* and the highest in *Arthromeris lehmanni*. The size of the epidermal cells of both abaxial and adaxial surfaces has been tabulated for all the species. The position of the stomata varied, in some species, it was clearly visible along with the epidermal cells whereas deeply sunken in species like *Arthromeris wallichiana*, *Lepisorus contortus*, *Lepisorus loriformis*, *Microsorum punctatum*, *Pyrrosia lanceolata* and *Pyrrosia mannii*. However, it was possible in all cases to distinguish subsidiary cells from other epidermal cells. In the studied taxa, mostly 6 different types of stomata namely, polocytic, copolocytic, seppolocytic (*Loxogramme involuta*), anisocytic (*Lepisorus rostratus*), pericytic, and copericytic (*Pyrrosia heteractis*) were observed (Figure 7-9). The epidermal cell types were mostly sinuous and broadly lobed or angular. The qualitative and quantitative epidermal characters of all the examined species have been presented in Table 4.

Key to the studies species based on leaf architecture, venation pattern and epidermal features

1a. Leaves simple, margin entire.. 2

b. Leaves compound, margin entire or toothed..................... 16

2a. Secondary venation reticulodromous.................................. 3

b. Secondary venation brochidodromous, weak brochidodromous or festooned brochidodromous 7

3a. Tertiary venation free forked 4

b. Tertiary venation opposite percurrent .... ***Loxogramme involuta***

4a. Primary vein size stout, secondary vein spacing uniform, quaternary venation random reticulate..... ***Pyrrosia costata***

b. Primary vein moderate, secondary vein spacing uniform or irregular, quaternary venation absent................................. 5

5a. Secondary vein spacing irregular or uniform, copericytic or pericytic stomata 6

b. Secondary vein spacing uniform, polocytic stomata .... ***Pyrrosia mannii***

6a. Secondary vein spacing uniform, looped marginal ultimate venation ....***Pyrrosia heteractis***

b. Secondary vein spacing irregular, incompletely looped marginal ultimate venation ....***Pyrrosia lanceolata***

7a. Primary vein size stout, tertiary venation opposite per current venation... 8

b. Primary vein size moderate, tertiary venation random reticulate or dichotomising 9

8a. Variation in angle of divergence of secondary veins is regular, freely ending veinlets 1-branched, looped marginal ultimate venation................... ***Microsorum membranaceum***

b. Variation in angle of divergence of secondary veins of upper veins slightly acute than lower, freely ending veinlets 2 or more branched, incomplete looped marginal ultimate venation .... ***Microsorum punctatum***

9a. Secondary venation brochidodromous, weak brochidodromous or festooned brochidodromous or indistinct, presence of looped marginal ultimate venation 10

b. Secondary venation weak brochidodromous, presence of a marginal secondary vein as marginal ultimate venation ....***Selliguea griffithiana***

10a. Leaf blade class nanophyll, leaf shape elliptic, cyclocytic stomata .... ***Lepisorus rostratus***

b. Leaf blade class microphyll to mesophyll, leaf shape linear lanceolate to broadly lanceolate, polocytic or copolocytic stomata 11

11a. Secondary venation weak brochidodromous,tertiary venation random reticulate.. 12

b. Secondary venation indistinct or brochidodromous or festooned brochidodromous, tertiary veins random reticulate or dichotomizing.. 13

Table 2. Qualitative venation details of the studied taxa.

Species	Primary Veins		Secondary Veins				Tertiary Veins Category	Quaternary Veins Category	F.E.V.S.	Marginal ultimate venation
	Category	Size	Category	Spacing	AD	VAD				
Art him	pinnate	moderate	weak brochidodromous	uniform	wide	Regular	random reticulate	dichotomizing	1-branched	marginal secondary vein
Art leh	pinnate	moderate	weak brochidodromous	uniform	wide	regular	random reticulate	dichotomizing	1 -branched	marginal secondary vein
Art wal	pinnate	moderate	weak brochidodromous	uniform	right angle	regular	random reticulate	dichotomizing	unbranched	marginal secondary vein
Dry pro	pinnate	stout	reticulodromous	uniform	wide	regular	random reticulate	opposite percurrent	unbranched	marginal secondary vein
Dry que	pinnate	moderate	festooned brochidodromous	uniform	wide	regular	random reticulate	alternate percurrent	unbranched	marginal secondary vein
Gon arg	pinnate	moderate	semicraspedodromous	uniform	wide	regular	absent	absent	unbranched	free forked
Lep con	pinnate	moderate	indistinct	random	acute	irregular	random reticulate	dichotomizing	unbranched	looped
Lep lor	pinnate	moderate	weak brochidodromous	irregular	acute	upper vein slightly acute than lower	random reticulate	dichotomizing	unbranched	looped
Lep meh	pinnate	moderate	festooned brochidodromous	uniform	wide	regular	random reticulate	dichotomizing	1-branched	looped
Lep nor	pinnate	moderate	weak brochidodromous	irregular	acute	irregular	random reticulate	free	unbranched	looped
Lep nud	pinnate	moderate	festooned brochidodromous	uniform	wide	regular	dichotomising	dichotomizing	unbranched	looped
Lep ros	pinnate	moderate	weak brochidodromous	uniform	wide	upper vein slightly acute than lower	random reticulate	dichotomizing	unbranched	looped
Lep sub	pinnate	moderate	brochidodromous	uniform	acute	upper vein slightly acute than lower	random reticulate	free	unbranched	looped
Lox inv	pinnate	moderate	reticulodromous	uniform	acute	regular	opposite percurrent	dichotomizing	absent	looped
Mic mem	pinnate	stout	weak brochidodromous	uniform	wide	regular	opposite percurrent	dichotomizing	1-branched	looped
Mic pun	pinnate	stout	weak brochidodromous	uniform	wide	upper veins slightly acute than lower	opposite percurrent	dichotomizing	2 or more branched	incomplete loops
Phy cus	pinnate	moderate	brochidodromous	uniform	wide	upper vein slightly acute than lower	dichotomising	absent	1-branched	looped
Phy sco	pinnate	stout	weak brochidodromous	irregular	wide	upper veins more acute than lower	random reticulate	dichotomizing	1-branched	looped
Pic ebe	pinnate	moderate	weak brochidodromous	uniform	wide	upper veins slightly acute than lower	random reticulate	absent	1-branched	marginal secondary vein

(Continued)

Species	Primary Veins		Secondary Veins				Tertiary Veins	Quaternary Veins	F.E.V.S.	Marginal ultimate venation
	Category	Size	Category	Spacing	AD	VAD	Category	Category		
Pic ste	pinnate	moderate	weak brochidodromous	uniform	wide	regular	random reticulate	absent	1-branched	marginal secondary vein
Pol amo	pinnate	moderate	semicraspedodromous	uniform	wide	regular	absent	absent	1-branched	free forked
Pyr cos	pinnate	stout	reticulodromous	uniform	wide	upper vein slightly acute than lowe	free forked	random reticulate	1-branched	incomplete loops
Pyr het	pinnate	moderate	reticulodromous	uniform	wide	upper vein slightly acute than lower	free forked	absent	unbranched	looped
Pyr lan	pinnate	moderate	reticulodromous	irregular	wide	upper vein slightly acute than lower	free forked	absent	unbranched	incomplete loops
Pyr man	pinnate	moderate	reticulodromous	uniform	wide	upper vein slightly acute than lower	free forked	absent	unbranched	incomplete loops
Sel gri	pinnate	moderate	weak brochidodromous	uniform	wide	regular	random reticulate	dichotomizing	1-branched	marginal secondary vein
Sel oxy	pinnate	moderate	weak brochidodromous	uniform	wide	regular	random reticulate	dichotomizing	1-branched	marginal secondary vein

Key: AD-Angle of Divergence; VAD-Variation in Angle of Divergence; F.E.V.S-Freely Ending Veinlet(s).

Table 3. Quantitative characters of areoles and veins of the studied taxa.

Species	Mean areole size (mm^2)	Veinlet entering areole/mm^2	Vein termination/ mm^2
Art him	3.04±0.2	2-3	1-2
Art leh	3.69±0.7	3-5	1-2
Art wal	5.98±0.4	3-5	1-2
Dry pro	3.22±0.2	0-1	1
Dry que	1.20±0.1	0-2	1-3
Gon arg	12.23±0.3	1	1
Lep con	2.9±0.09	1-2	1
Lep lor	16.01±0.5	1-3	1
Lep meh	8.75±0.4	3-4	1-2
Lep nor	5.24±1.0	1-2	1
Lep nud	2.34±0.1	1-3	1-2
Lep ros	4.75±0.2	3-4	1
Lep sub	5.63±0.2	1-2	1
Lox inv	13.3±1.4	1-3	1-2
Mic mem	12.6±1.0	3-4	1-2
Mic pun	2.52±0.2	1-2	1-2
Phy cus	3.5±0.6	1-3	1
Phy sco	0.5±0.04	1-4	1
Pic ebe	3.9±0.2	1-2	1
Pic ste	2.42±0.1	1-2	1-2
Pol amo	9.06±2.2	1	1
Pyr cos	4.16±0.3	1-2	1-2
Pyr het	3.95±0.4	3-5	1-2
Pyr lan	2.38±0.18	2-3	1-2
Pyr man	10.61±0.9	3-4	1
Sel gri	2.33±0.1	2-6	1
Sel oxy	6.31±0.4	2-4	1-2

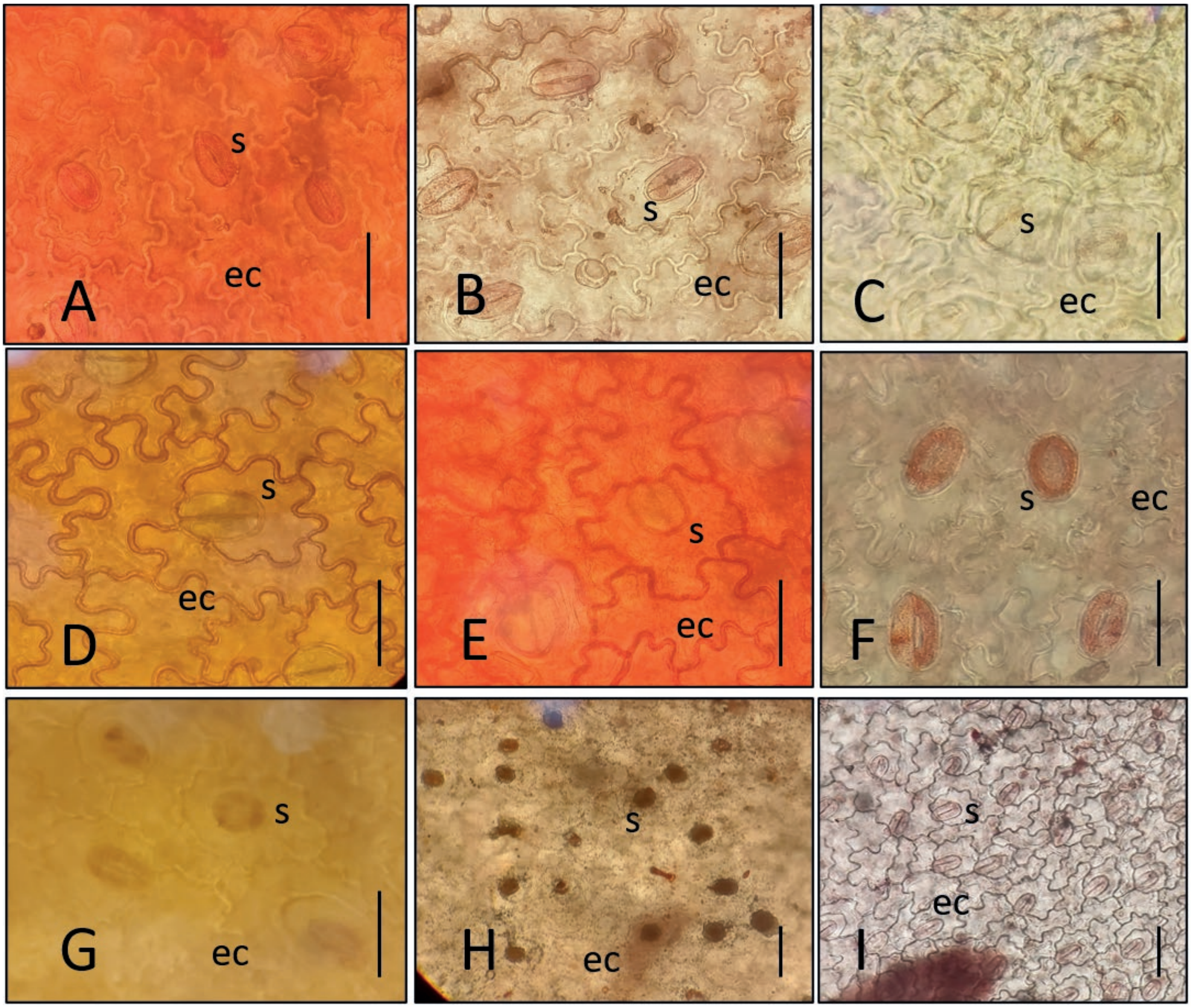

Figure 7. Leaf epidermis with stomata in Polypodiaceae: **A**-*Arthromeris himalovata*; **B**-*Arthromeris lehmanii*; **C**-*Arthromeris wallichiana*; **D**-*Drynaria quercifolia*; **E**-*Drynaria propinqua*; **F**-*Goniophlebium argutum*; **G**-*Lepisorus contortus*; **H**-*Lepisorus loriformis*; **I**-*Lepisorus mehrae* (Key: s-stomata; ec-epidermal cell; Scale bar-25µm).

12a. Secondary vein angle of divergence irregular, quaternary veins free .... ***Lepisorus normalis***

b. Secondary vein angle of divergence of upper veins slightly acute than lower, quaternary veins dichotomizing .... ***Lepisorus loriformis***

13a. Secondary venation indistinct, secondary vein spacing random, tertiary venation random reticulate .... ***Lepisorus contortus***

b. Secondary venation brochidodromous or festooned brochidodromous, secondary vein spacing uniform 14

14a. Brochidodromous secondary venation, secondary venation angle of divergence of upper vein slightly acute than lower, tertiary venation random reticulate, quaternary veins free .... ***Lepisorus sublinearis***

b. Festooned brochidodromous secondary venation, secondary venation angle of divergence regular, tertiary venation random reticulate or dichotomizing, quaternary veins dichotomising 15

15a. Tertiary veins random reticulate, freely ending veinlets 1-branched .... ***Lepisorus mehrae***

b. Tertiary veins dichotomizing, freely ending veinlets unbranched .... ***Lepisorus nudus***

16a. Secondary venation semicraspedodromous, tertiary venation absent 17

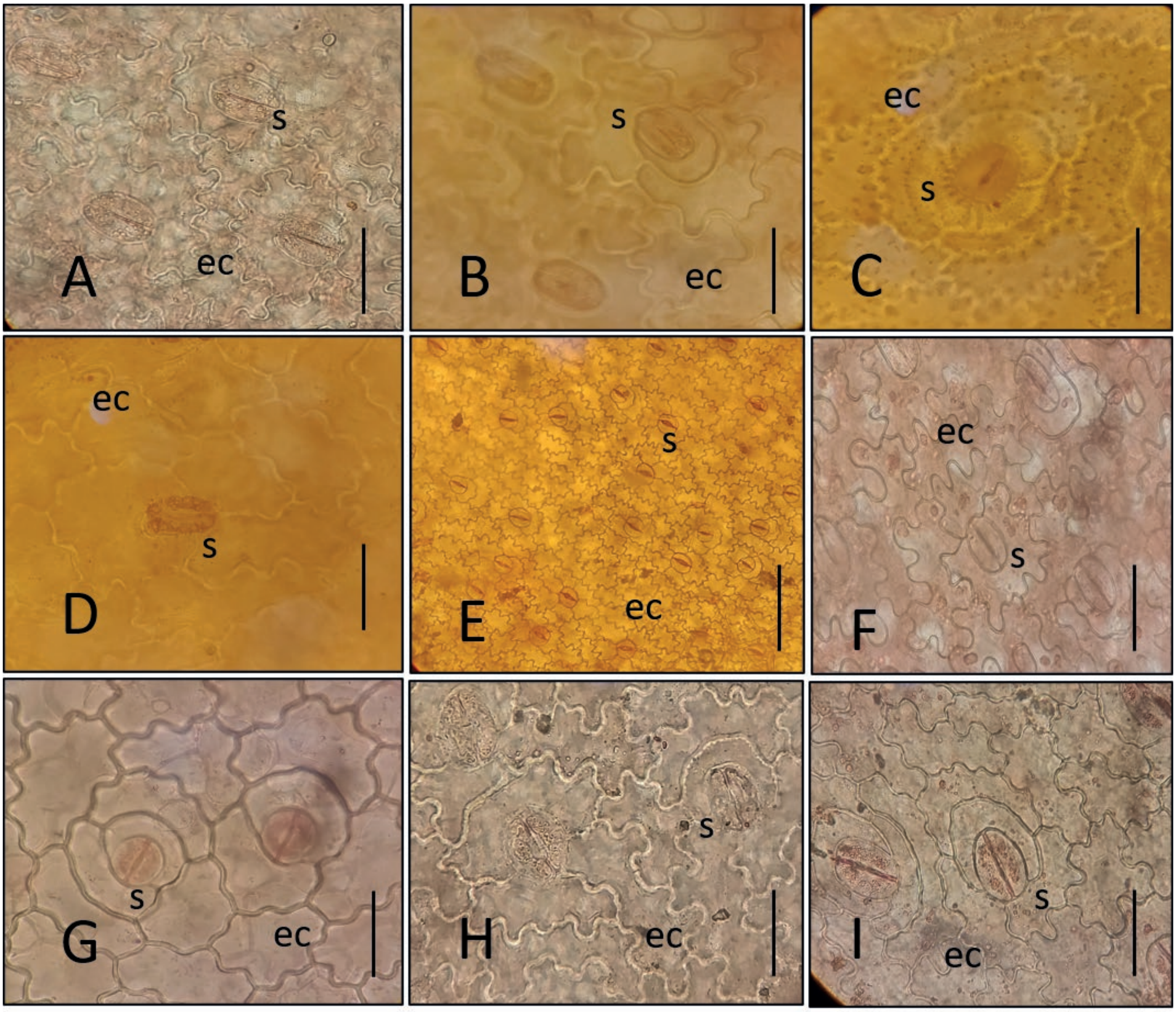

Figure 8. Leaf epidermis with stomata in Polypodiaceae: **A**-*Lepisorus normalis;* **B**-*Lepisorus nudus*; **C**-*Lepisorus rostratus*; **D**-*Lepisorus sublinearis*; **E**-*Loxogramme involuta*; **F**-*Microsorum membranaceum*; **G**-*Microsorum punctatum*; **H**-*Phymatosorus cuspidatus*; **I**-*Phymatosorus scolopendria* (Key: s-stomata; ec-epidermal cell; Scale bar-25µm)

b. Secondary venation reticulodromous, brochidromous, festooned brochidodromous or weak brochidodromous, tertiary venation present 18

17a. Lamina division 1-pinnate, leaf margin mucronate............ .... ***Goniophlebium argutum***

b. Lamina division deeply pinnatifid, leaf margin serrate ....***Polypodiodes amoena***

18a. Primary vein size stout, lamina division pinnatifid, secondary venation reticulodromous.......***Drynaria propinqua***

b. Primary vein size moderate, lamina division pinnafid, deeply pinnatifid, palmafid, 1-pinnate or imparripinate, secondary venation brochidodromous, weak or festooned brochidodromous 19

19a. Secondary venation brochidromous, lamina division imparipinnate................................***Phymatosorus cuspidatus***

b. Secondary venation weak brochidodromous or festooned brochidodromous, lamina division 1-pinnate or pinnatifid...... 20

20a. Secondary venation festooned brochidodromous,tertiary venation random reticulate, quaternary vein alternate percurrent, lamina division pinnatifid .... ***Drynaria quercifolia***

b. Secondary venation weak brochidodromous, tertiary venation present or absent 21

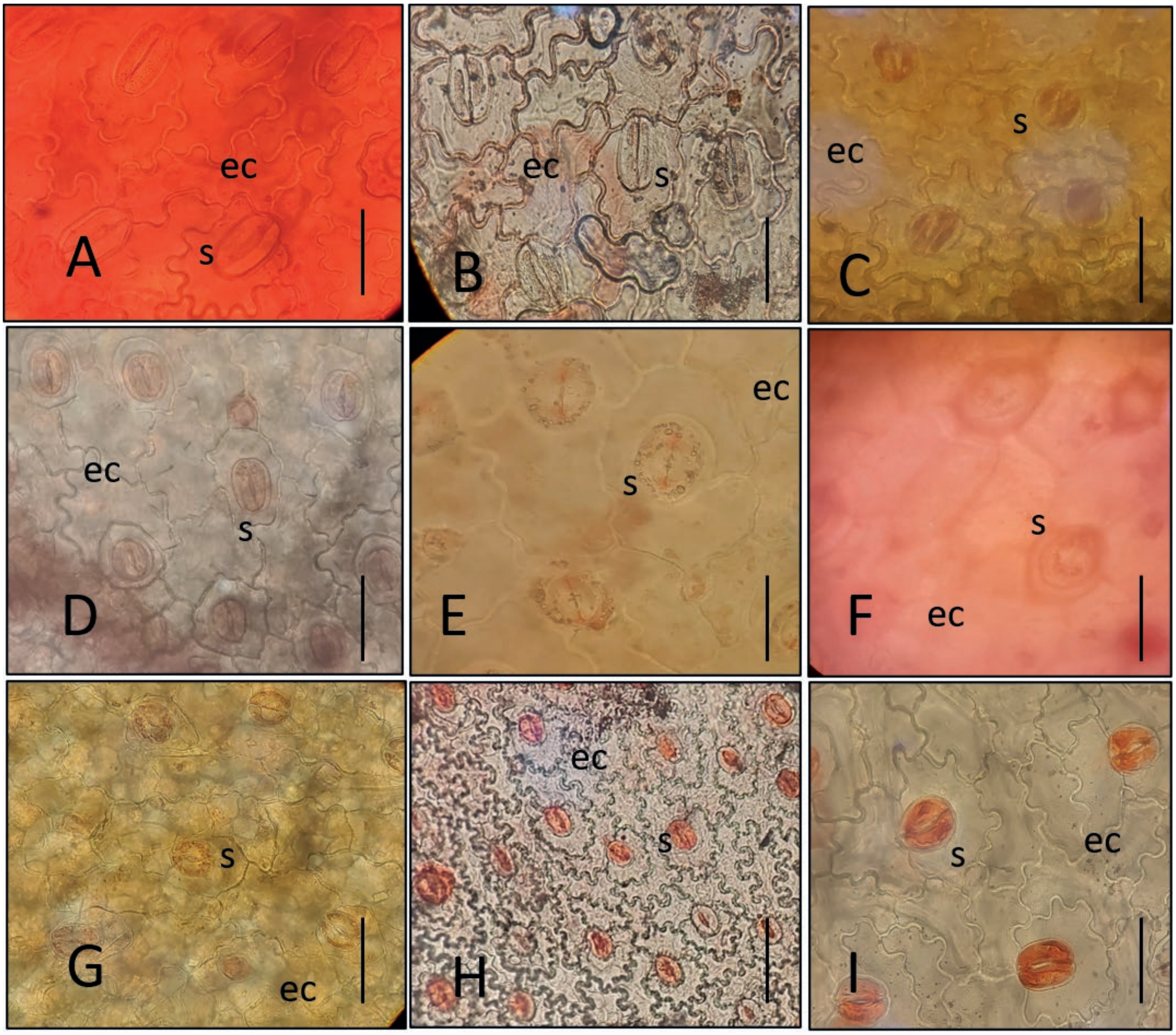

Figure 9. Leaf epidermis with stomata in Polypodiaceae: **A**-*Pichisermollodes ebenipes;* **B**-*Pichisermollodes stewartii*; **C**-*Polypodoides amoena*; **D**-*Pyrrosia costata*; **E**-*Pyrrosia heteractis*; **F**-*Pyrrosia lanceolata*; **G**-*Pyrrosia mannii*; **H**-*Selliguea griffithiana*; **I**-*Selliguea oxyloba* (Key: s-stomata; ec-epidermal cell; Scale bar-25μm).

21a. Tertiary venation present 23

b. Tertiary venation absent 22

22a. Lamina division pinnately parted, secondary venation angle of divergence regular......***Pichisermollodes stewartii***

b. Lamina division palmatifid, secondary venation angle of divergence upper veins slightly acute than lower .... ***Pichisermollodes ebenipes***

23a. Secondary vein spacing irregular, tertiary venation random reticulate, quaternary venation absent .... ***Phymatosorus scolopendria***

b. Secondary vein spacing uniform,tertiary venation random reticulate, quaternary venation present 24

24a. Lamina division deeply pinnatifid, leaf margin entire, mean areole size greater than ±6mm^2 .... ***Selliguea oxyloba***

b. Lamina division 1-pinnate, leaf margin entire or minutely toothed, mean areole size lesser than ±2-5 mm^2 25

25a. Leaf base rounded, Angle of divergence in secondary veins are wider angle (≥90°) 26

b. Leaf base obliquely cordate, Angle of divergence in secondary veins are at right angle (90°)..***Arthromeris wallichiana***

Table 4. Detailed epidermal and stomatal cell characteristics of the studied taxa.

Species	Surface	EC wall type	ECL (µm)	ECW (µm)	Lobes per cell	ST type(s)	STL (µm)	STW (µm)	STS (µm^2)	SI
Art him	AB	sinuous	26.8±0.4	16±0.5	5-8	copolocytic, polocytic	18.5±0.6	14.2±0.2	267±0.8	30.75±0.1
	AD	sinuous	27.5±0.3	16.2±0.4	6-10					
Art leh	AB	sinuous	35.6±0.9	20±1.1	6-9	polocytic, copolocytic	20±0.4	18.5±0.3	370±0.6	46.15±0.3
	AD	sinuous	37±0.5	22.3±0.7	7-10					
Art wal	AB	sinuous	29±0.8	17.5±0.9	4-10	polocytic	19±0.3	15.5±0.0	294.5±0.1	29.51±0.2
	AD	sinuous	30±0.3	18.6±0.6	4-11					
Dry pro	AB	sinuous	52.5±0.4	32.5±0.5	6-10	polocytic	32±2.1	17±0.9	544±0.8	26.66±0.1
	AD	sinuous	55±0.4	33.5±0.4	5-10					
Dry que	AB	sinuous	75±0.9	40±0.3	6-10	polocytic, copolocytic	25±1.3	22.5±1.2	562.5±0.9	25.78±0.3
	AD	sinuous	77.3±0.6	42±0.7	6-10					
Gon arg	AB	sinuous	57.5±1.1	40±0.9	8-12	polocytic, copolocytic	33±0.6	29±0.3	957±1.0	22.22±0.1
	AD	sinuous	57±0.2	43±0.1	10-12					
Lep con	AB	sinuous	110.9±0.8	45±0.6	6-7	copolocytic, polocytic	37±0.5	23.5±0.4	869.5±0.3	20.5±0.3
	AD	sinuous	115±0.6	38.33±0.2	6-9					
Lep lor	AB	slightly lobed	75.26±2.9	24±2.4	3-4	copolocytic, polocytic	28±0.3	21±0.2	588±0.5	15.9±0.4
	AD	sinuous	78±1.8	26.8±0.3	5-7					
Lep meh	AB	sinuous	55±1.7	34±1.1	4-5	polocytic, copolocytic	23.5±0.5	19±0.5	446.5±0.5	40±0.1
	AD	sinuous	53±1.9	35±1.3	4-7					
Lep nor	AB	sinuous	65.4±0.3	38.11±0.0	5-6	copolocytic, polocytic	32.7±0.1	25±0.4	817.5±0.3	30.5±0.2
	AD	sinuous	66±0.4	40±0.5	5-6					
Lep nud	AB	sinuous	60±3.2	55.2±0.4	4-8	copolocytic, polocytic	44±0.2	27±0.3	1188±0.2	20.5±0.1
	AD	sinuous	61±2.1	53.6±0.8	4-9					
Lep ros	AB	sinuous	48.83±0.4	33±4.3	8-10	cyclocytic	27.3±2.8	19±2.1	518.7±0.9	24±0.1
	AD	straight	48±0.5	31±1.8	-					
Lep sub	AB	sinuous	51±0.5	35±2.3	4-6	polocytic	25.4±0.7	12.3±1.7	304±0.4	18.18±0.2
	AD	slightly lobed	53±0.7	35.5±0.1	5-7					
Lox inv	AB	sinuous	45±0.3	33.3±0.2	6-10	seppolocytic	48.3±0.1	33.8±0.3	1584±0.6	9.04±0.1
	AD	sinuous	44±0.2	32±0.6	6-12					
Mic mem	AB	sinuous	75±1.1	35±0.3	4-6	polocytic	31±0.2	19±0.3	589±0.2	14.76±0.3
	AD	sinuous	77±0.5	34.4±0.2	4-6					
Mic pun	AB	sinuous	63.2±0.4	33.2±0.6	4-8	polocytic	33±1.9	20±0.7	660±1.1	16.66±0.1
	AD	sinuous	65.4±0.4	31.7±0.4	5-10					
Phy cus	AB	sinuous	53±0.3	34±0.2	5-8	copolocytic, polocytic	32±0.7	23.7±0.5	752±0.3	19.14±0.2
	AD	sinuous	50.2±0.6	35±0.7	5-10					
Phy sco	AB	sinuous	61±1.7	30.64±0.3	8-12	copolocytic, polocytic	30.33±0.2	21.02±1	637.53±0.3	24.22±0.1
	AD	sinuous	58.9±1.9	30.1±0.5	8-14					
Pic ebe	AB	sinuous	84.5±1.1	43±3.6	8-10	copolocytic, polocytic	28±0.5	21.5±0.8	602±0.4	33.33±0.1
	AD	sinuous	82.3±0.4	40±4.3	8-12					
Pic ste	AB	sinuous	65.9±2.3	22±1.7	5-8	polocytic	31±0.8	21±0.4	651±1.1	21.67±0.2
	AD	sinuous	66.2±2.1	21.5±0.7	6-10					
Pol amo	AB	sinuous	55.7±0.2	43.5±0.1	5-8	polocytic	35±0.4	23.5±1.3	822.5±0.7	25.49±0.1
	AD	sinuous	56±0.2	43±0.5	5-9					
Pyr cos	AB	slightly lobed	85.3±0.7	25.6±0.2	-	pericytic	29±0.2	17±0.5	493±0.1	25.8±0.1
	AD	slightly lobed	88.6±0.5	24±0.3	-					
Pyr het	AB	slightly lobed	66.2±0.7	28±0.5	-	copericytic, pericytic	23.5±0.1	19±0.8	446.5±0.2	20.45±0.3
	AD	slightly lobed	65.4±1.2	26.8±0.5	-					
Pyr lan	AB	straight	77.5±0.5	26.2±0.9	-	pericytic	28.5±0.6	19±1.7	541.5±0.4	13.51±0.1
	AD	straight	79.2±0.4	28±1.1	-					
Pyr man	AB	straight	29±0.8	21.5±1.7	-	polocytic	19.5±0.4	13.5±1,1	263.25±0.4	18.6±0.2

(Continued)

Species	Surface	EC wall type	ECL (μm)	ECW (μm)	Lobes per cell	ST type(s)	STL (μm)	STW (μm)	STS (μm²)	SI
	AD	straight	30.12±0.7	21±0.7	-					
Sel gri	AB	sinuous	71±2.3	48±0.6	8-14	polocytic	29±3.6	11.5±0.4	333.5±0.3	16.67±0.1
	AD	sinuous	73±2.1	52.7±0.9	8-16					
Sel oxy	AB	sinuous	75±0.6	30±0.2	7-12	polocytic	20±2.9	16±0.3	320±0.2	16±0.4
	AD	sinuous	78±0.8	33.3±3.6	8-12					

Key: AB-Abaxial; AD-Adaxial; ECL-epidermal cell length; ECW-epidermal cell width; STL-Stomatal length; STW-Stomatal width; STS-Stomatal size; SI-Stomatal index. All measurements expressed as mean ± standard error.

26a. Leaf shape ovate-lanceolate, leaf apex shape caudate, leaf margin entire, 2-3 veinlet entering areole per .... ***Arthromeris himalovata***

b. Leaf shape lanceolate, leaf apex shape acuminate, leaf margin minutely toothed, 3-5 veinlet entering areole per mm² .... ***Arthromeris lehmannii***

A UPGMA dendrogram based on similarity was obtained from the quantitative and qualitative data analysed during the study (Figure 10). The inter relationship between the taxon can be understood. Higher degree of similarity (≥0.95) was observed between *Drynaria propinqua* and *Drynaria quercifolia*, *Lepisorus contortus* and *Lepisorus sublinearis* and *Microsorum membranaceum, Microsorum punctatum* and *Pyrrosia costata.* Over 90% similarity has been observed between *Goniophlebium argutum* and *Polypodoides amoena* while *Lepisorus rostratus* and *Lepisorus loriformis* show ≤ 0.85 similarity with other *Lepisorus* species. *Loxogramme involuta* shares ≤ 0.70 of similarity with the rest of the Polypodiaceous species.

DISCUSSION

Fern leaf or frond shares a common character which is the presence of a stalk and a lamina. However, the leaves exhibit a wide diversity, especially in size and shape (Vasco et al. 2013). Christenhusz and Chase (2014) suggested that families under eupolypods I clade have enormous morphological diversity thus leading to the difficulty to visualise the group as a single clade. From our study, it can be observed that such diverse characteristics exists even within the species of Polypodiaceae which is a part of the eupolypods I. Polypodiaceous ferns exhibited variable morphological characters such as lamina division, shape, leaf blade class, and margin. The morphological traits prove to be more effective in taxonomic delineation if supported by other stable characters such as leaf venation (Magrini and Scoppola 2010; Sundue and Rothfels 2014; Tan and Buot 2020).

On examination of the leaf venation traits, it has been observed that the 27 representative species of family Polypodiaceae possess pinnate type of primary venation and the variations mostly occur in the higher degree vein order. The higher venation character offers great taxonomic value (Sack and Scoffoni 2013; Tan and Buot 2020).

The overall species in our study exhibited weak brochidodromous (11 species), festooned brochidodromous (three species), brochidodromous (two species), reticulodromous (seven species), and two species with semi craspedodromous secondary venation pattern. Species showed nearly uniform in terms of variation in angle of divergence. Those species having weak brochidodromous and reticulodromous secondary vein usually had upper veins more acute than lower veins in terms of variation in angle of divergence.

Similar results were observed from earlier works (Conda and Buot 2018; Tan and Buot 2019; Tan and Buot 2020), in which ferns differed in 2° vein, 3° vein, 4° vein, angle of divergences of the secondary veins, and areolation. In works of Tan and Buot (2019), semi-craspedodromous secondary veins were observed in *Goniophlebium subauriculatum*. In our study, *Goniophlebium argutum* and *Polypodoides amoena* exhibited semi-craspedodromous 2° venation. They also have similar polocytic stomatal type. The dendrogram obtained also reveals more than 90% similarity between the two species. Therefore, it supports the fact that the *Polypodoides amoena* and *Goniophlebium amoenum* are homotypic synonyms.

The epidermal cells generally vary in size and shape among the studied taxa. The shape of epidermal cells is mostly irregular. The anticlinal walls are slightly lobed and sinuous. The shape of anticlinal wall of epidermal cells is a result of environmental adaptation, mesophytic species generally have sinuous walls while xerophytes have straight walls (Gifford 1989). Majority of *Pyrrosia* species are extremely drought tolerant with xerophytic adaptations (Wei et al. 2017). In our study, we observed epidermal cells with straight walls in *Pyrrosia lanceolata*

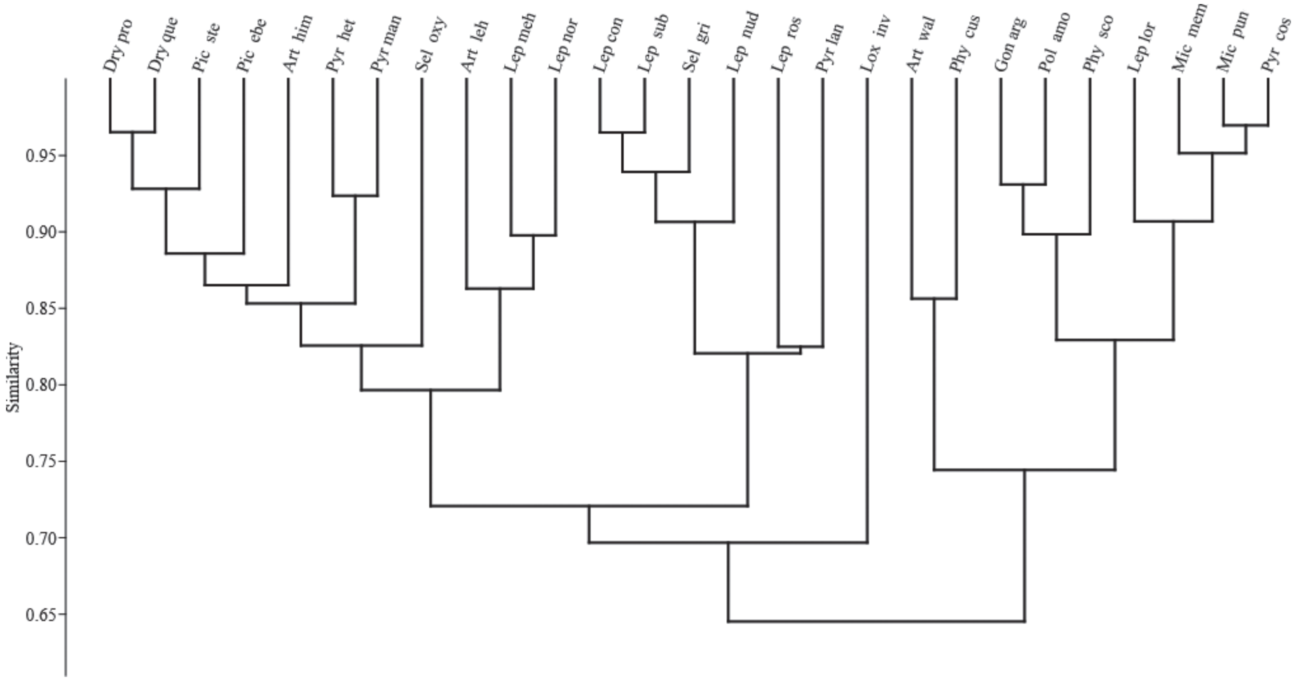

Figure 10. UPGMA dendrogram based on similarity among the studied taxa.

and *Pyrrosia mannii*. Fern leaves are mostly hypostomatic (Wang et al. 2009; Deng and Wang 2010; Shah et al. 2018). All the species possess stomata only on abaxial surface. From the variations observed, it is seen that most of the Polypodiaceae ferns have Polocytic, copolocytic, pericytic type of stomata. *Loxogramme involuta,* mostly exhibit seppolocytic type of stomata with lower stomatal index compared to the rest of the studied taxa. In the works of Van Cotthem (1970) and Pichi-Sermolli (1970), stomatal features have been used to differ Grammitidaceae and Loxogrammaceae from Polypodiaceae, however, it was not confirmed by Sen and Hennipman (1981). Molecular data consistently indicate that *Loxogramme* is sister to the rest of the Polypodiaceae (Schneider et al. 2004; Kreier and Schneider 2006; Wei et al. 2021). In our study, it is can be visualised from the dendrogram that *Loxogramme involuta* shares lesser than 0.70 similarity from rest of the Polypodiaceous taxa. Molecular studies consistently suggests that Loxogrammoid ferns are sister to the rest of the Polypodiaceae (Schneider et al.2004; Wei and Zhang 2022).

According to the new classification of *Lepisorus* proposed by Zhao et al. (2020), *Tricholepidium normale* (D.Don) Ching and *Lemmaphyllum rostratum* (Bedd.) Tagawa are now considered homotypic synonyms of *Lepisorus normalis* (D.Don) C.F.Zhao, R.Wei & X.C. Zhang and *Lepisorus rostratus* (Bedd.) C.F.Zhao, R.Wei & X.C.Zhang (Wei and Zhao 2019). Combined molecular studies showed that *Lepisorus* were recovered to be monophyletic when *Tricholepidium*, *Lemmaphyllum*, *Neolepisorus* and some other related genera were included (Zhao et al. 2020). The stomatal type of *Lepisorus normalis* varies from copolocytic to polocytic as in all other *Lepisorus* species in our study. However, cyclocytic stomatal type has been observed in *Lepisorus rostratus* which is quite different from the rest. In recent studies with some *Lepisorus* species by Mondal and Moktan (2022), it was observed that *Lepisorus rostratus* was out-grouped from the rest of the studied taxa based on significant morpho-anatomical features. Although the secondary and higher venation orders, the epidermal cell sizes, the stomatal index is closer to the other species of these genera. Though the mature stomata in the polypodioid ferns show different forms, all of them go through the polocytic conditions during their development. One such lines of development lead to the formation of cyclocytic and cocyclocytic stomata. The other line is characterised by the formation of stomata types like desmocodesmocytic, peri-, and copericytic forms (Sen and Hennipman 1981).

The reticulodromous venation with frees forked tertiary veins having pericytic and co pericytic stomatal type (*P. mannii* being exception in having polocytic stomata) makes *Pyrrosia* genus distinct from other members of Polypodiaceae. The origin and relationship of the genus has been debated among pteridologists. Christensen (1938) and Copeland (1947), associated *Pyrrosia* with Pleopeltoid group of ferns of the Polypodiaceae, whereas Copeland considered it closer to the microsorioid group. Based on phylogenetic analyses the infrageneric classification of *Pyrrosia s.l.* is controversial. Reticulate evolution was suggested among the species (Wei et al. 2017). The predominant pericytic stomata type in *Pyrrosia s.l.* is a recent adaptive feature in Polypodiaceae. Some species of *Pyrrosia* still have polocytic stomata, which are observed in other genera of Polypodiaceae. The occurrence of polocytic stomata in *Pyrrosia* may be due to the reversion or secondary development (Wei et al. 2017).

Ching (1978), established sub-family Lepisoroideae replacing Pleopeltidoideae and Pyrrosioideae. Raised several subfamilies like Gymnogrammitis (Gymnogrammitidaceae), *Drynaria* (Drynariaceae), and *Platycerium* (Platyceriaceae) to the family level. Later, phylogenetic studies based on multiple parameters provided better comprehension of the familial and generic circumscription of Polypodiaceae (Schneider et al. 2004; Schuettpelz and Pryer, 2007; Kreier et al. 2008; Testo et al. 2019; Zhao et al. 2020).

Major classifications by Smith et al. (2006), Christenhusz et al. (2011) and PPG I (2016), settled with a broader definition of Polypodiaceae by considering several closely associated groups like Loxogrammoids, Grammitids, Drynariaceae, and Platyceriaceae. Similar inter relationship between the taxon can be understood from the UPGMA obtained in this investigation. In our present study based on the leaf venation patterns reveals that higher degree of similarity (≥ 0.95) was observed between *Microsorum membranaceum* and *Microsorum punctatum* as species belonging to the same genera usually possess the same pattern of stomata, leaf venation, lamina division etc. A phylogenetic and morphological analyses conducted by Testo et al. 2019 proposed two new genera *Bosmania* and *Zealandia* under subfamily Microsoroideae of Polypodiaceae family. *Microsorum membranaceum* was shifted to the genera *Bosmania* therefore *Bosmania membranacea* (D.Don) Testo and *Microsorum membranaceum* (D.Don) Ching are homotypic synonyms (Testo et al. 2019).

Over 90% similarity has been observed between *Goniophlebium argutum* and *Polypodoides amoena* which is quite evident in their secondary venation pattern being semicraspedodromous type which is distinct from rest of the studied taxa. *Lepisorus rostratus* and *Lepisorus loriformis* shows lesser than 85% similarity with other *Lepisorus* species. *Loxogramme involuta* shares around 70 % similarity with rest of the Polypodiaceae species. The reticulodromous secondary venation pattern as well as stomatal type being seppolocytic is less observed in Polypodiaceae.

Therefore, it is evident from the study that leaf micro-morphological details and venation patterns can serve as an additional set of data in line with molecular and morphological characters which could help in decoding the existing problems up to generic and specific levels. The combination of diagnostic morphological characters like rhizome scales, leaf shapes, venation patterns, and features of the paraphyses proved crucial in untangling the clades and sub-clades of genus *Lepisorus, Pleopeltis*, and the grammatid ferns (Ranker et al. 2004; Otto et al. 2009; Wang et al. 2010; Zhao et al. 2020).

CONCLUSION

The present investigation reveals that leaf architectural traits and venation patterns especially higher degree veins are useful characters in delineating species. It can be concluded that features like leaf venation and stomata type is genetically stable and related to ontogeny and phylogeny. The results can serve as an additional and complementary data for the ferns under Polypodiaceae family. It is a reliable and economical tool in identification and classification of fern taxa. It is suggested that other fern species can be explored and classified precisely through leaf architectural approaches.

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Supplementary file. Voucher specimens used for the foliar micro-morphological study.

Species	Voucher number	Collector(s)	Locality	Habitat	Date
Arthromeris himalovata	SM-0358	S Mondal, S Moktan	Third mile	Epiphyte	15/10/2020
Arthromeris lehmannii	SM-0360	S Mondal, S Moktan	Sixth mile	Lithophyte or epiphyte	16/10/2020
Arthromeris wallichiana	SM-0363	S Mondal	Third mile	Lithophyte or epiphyte	16/10/2020
Drynaria propinqua	SM-0501	S Mondal	Kurseong	Epiphyte or lithophyte	22/09/2021
Drynaria quercifolia	SM-0550	S Mondal	Sukna	Lithophyte or epiphyte	27/09/2021
Goniophlebium argutum	SM-0582	S Mondal	Jorebunglow	Epiphyte or lithophyte	29/09/2021
Lepisorus contortus	SM-0344	S Mondal	Third mile	Epiphyte	15/10/2020
Lepisorus loriformis	SM-0493	S Mondal, S Moktan	Kaiyakatta	Epiphyte	21/09/2020
Lepisorus mehrae	SM-0365	S Mondal	Mungpoo	Lithophyte or epiphyte	24/09/2020
Lepisorus normalis	SM-0599	S Mondal	Lebong	Epiphyte or lithophyte	29/09/2021
Lepisorus nudus	SM-0239	S Mondal	Lebong	Epiphyte or lithophyte	29/09/2021
Lepisorus rostratus	SM-0554	S Mondal, S Moktan	Rajahatta	Epiphyte or lithophyte	28/09/2021
Lepisorus sublinearis	SM-0324	S Mondal, S Moktan	Third mile	Epiphyte or lithophyte	14/10/2020
Loxogramme involuta	SM-0223	S Mondal, S Moktan	Mahanadi	Lithophyte or epiphyte	24/09/2020
Microsorum membranaceum	SM-0464	S Mondal, S Moktan	Lebong	Lithophyte	18/09/2021
Microsorum punctatum	SM-0512	S Mondal, S Moktan	Pankhabari	Epiphyte or lithophyte	23/09/2021
Phymatosorus cuspidatus	SM-0211	S Mondal	Rohini	Lithophyte	21/09/2020
Phymatosorus scolopendria	SM-0552	S Mondal	Sukna	Lithophyte or terrestrial	27/09/2021
Pichisermollodes ebenipes	SM-0315	S Mondal, S Moktan	Third mile	Epiphyte or lithophyte	14/10/2020
Pichisermollodes stewartii	SM-0614	S Mondal, S Moktan	Ghoom	Epiphyte or lithophyte	17/10/2021
Polypodiodes amoena	SM-0498	S Mondal	Kurseong	Epiphyte or lithophyte	22/09/2021
Pyrrosia costata	SM-0533	Mondal,S	Pankhabari	Lithophyte or epiphyte	23/09/2021
Pyrrosia heteractis	SM-0602	S Mondal	Bagora	Lithophyte or epiphyte	02/10/2021
Pyrrosia lanceolata	SM-0386	S Mondal	Rongtong	Lithophyte or epiphyte	18/09/2021
Pyrrosia mannii	SM-0546	S Mondal, S Moktan	Panighatta	Lithophyte or epiphyte	25/09/2021
Selliguea griffithiana	SM-0355	S Mondal	Third mile	Lithophyte or epiphyte	15/10/2020
Selliguea oxyloba	SM-0371	S Mondal	Senchal	Lithophyte or epiphyte	03/09/2021