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Investigating the leaf architecture of Eupolypods I (Polypodiales): implications to taxonomy

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ABSTRACT

The taxonomy of the leaf surface has been controversial due to plasticity of most characters. However, leaf architecture, a genetically fixed character was explored to generate characters that would effectively identify and describe species of eupolypods I, an unstable group of Polypodiales. Leaf architecture characters of the twenty-one (21) selected species, representing nine families of eupolypods I were examined and measured. The results showed that species of eupolypods I can be described based on general morphology such as leaf organization, leaf shape, size, and angle; and leaf venation characters such as primary vein, secondary vein, tertiary vein, quaternary vein, areoles, angle of divergence, variation in angle of divergence, and spacing. Indeed, leaf architecture is a significant tool in taxonomic study of eupolypods I.

Key words: Eupolypods I, leaf architecture, Polypodiales, venation.

INTRODUCTION

Eupolypods I, a subclade of eupolypods, includes nine families (Didymochlaenaceae, Hypodematiaceae, Davalliaceae, Nephrolepidaceae, Lomariopsidaceae, Tectariaceae, Oleandraceae, Dryopteridaceae and Polypodiaceae), 108 genera, and an approximate number of 4208 species (Smith et al. 2006; PPG 2016). These families are morphologically divergent and hence, identifying or unifying is extremely difficult and overwhelming.

Recently, molecular sequencing and spore morphology had been the subject of interest in systematics (Conda et al. 2017). However, this is not the ultimate solution for elucidating phylogenies (Tan & Buot 2019). Fortunately, there is a cheap and easy alternative, such as leaf architecture which measures gross morphology and leaf venation patterns, dubbed as genetically fixed (Hickey 1973, Roth-Nebelsick et al. 2001). Leaf architecture has been successful in identifying and describing, not only in angiosperms but in pteridophytes as well. Just like other vascular plants, ferns have distinct venation patterns (Conda et al. 2017). The rigidity offered by the thick sclerenchyma cells provide support for the architecture of the leaf, making it stable (Larcher et al. 2013). Thus, this study explored the use of leaf architecture in selected eupolypods I species. The objectives were to describe the leaf architecture characters of selected eupolypods I and to construct a dichotomous key to delineate species.

MATERIALS AND METHODS

Selection of Herbarium Specimens

The specimens examined for leaf architecture details are from the Philippine National Herbarium (PNH), Philippine University Herbarium (PUH) in the University of the Philippines Diliman; Museum of Natural History Herbarium, University of the Philippines Los Baños (CAHUP); and Plant Biology Division Herbarium (PBDH) of the Institute of Biological Sciences, University of the Philippines Los Baños. A total of twenty-one (21) well-pressed herbarium specimens were selected from the identified representative species of eupolypods I. Two to four (2-4) specimens of each representative species were examined with around 30 measurements per species. The representative species of each family were selected based on the type genus or other genus of each family available, following PPG I (2016). For species not available in the herbaria, a series of fieldworks in Mt. Makiling, Los Baños, Laguna; Quezon-Laguna UP Land Grant, and Mt. Mantalingahan, Palawan were done to collect samples. Specimens were pressed and deposited to the Plant Biology Division Herbarium (PBDH), University of the Philippines Los Baños. Vouchers were measured similar to those in herbaria mentioned previously. Additional information including exsiccatae, collection site, altitudinal variation, and habitat were noted.

Examination of Leaf Architecture

With the use of a stereo microscope and hand lens, thirty (30) mature pinna or pinnules from two to four herbarium specimens were considered. The specimens were described using leaf architecture terminologies and characters from Hickey (1973), Leaf Architecture Working Group (1999); Manual of Leaf Architecture (Ellis et al., 2009); and Conda & Buot (2018). A dichotomous key was generated using leaf architecture characters. An illustration of a typical fern structure is provided to understand the morphology and leaf architecture description (Fig. 1).

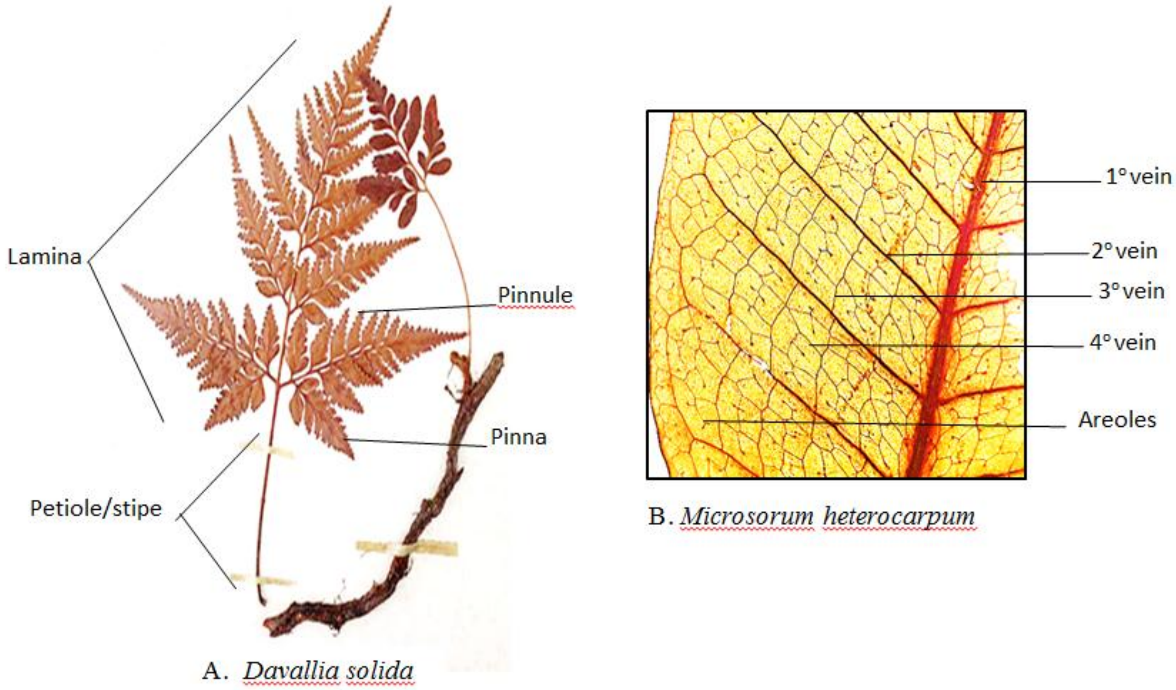

Fig. 1. Typical parts of a fern showing leaf parts (A) and venation characters (B).

To measure width and length of the lamina, a ruler and caliper were used; as well as protractor for the angle of divergence. The characters measured were patterned from Conda et al. (2017) as follows:

A. BLADE

1. Organization (simple, pinnate, tripinnate, pinnatifid, bipinnatifid, tripinnatifid)
2. Length (mm) – distance between the most proximal to the most distal portion of the leaf
3. Width (mm) – widest leaf of the pinna or pinnule
4. Area (mm2) – length x width x 2/3
5. L:W ratio – length divided by width
6. Blade class – determined by the area of the leaf in mm^2
7. Apex shape (straight, convex, rounded, truncate, acuminate, complex, retuse, emarginate, lobed)
8. Base shape (cuneate, convex, rounded, truncate, concave, decurrent, complex)
9. Base angle (acute, obtuse, wide obtuse)
10. Symmetry (symmetrical, asymmetrical)
11. Margin (entire, erose, crenate, serrate)
12. Lobation: unlobed or lobed (shallow, moderate, deep)

B. Primary (1^o) vein

1. Venation type: Pinnate

2. Primary vein size: (Massive, stout, moderate, weak)

C. Secondary 2^o vein

1. Venation pattern
a. Cladodromous – secondaries freely branching toward the margin
b. Craspedodromous – secondaries terminating at the margin
c. Semicraspedodromous – secondary veins branching just within the margin, one of the branches terminating at the margin and the other joining the superadjacent secondaries.
d. Reticulodromous – secondaries branching into a reticulum toward the margin
e. Weak brochidodromous – secondaries joined together in a series of arches
3. Secondary vein size: (Weak, moderate, stout, massive)
2. Angle of divergence- measured between the branch and the continuation of the source vein above the point of branching. Ranges of values shown in Table 2.
3. Variation in angle of divergence.
a. Divergence angle nearly uniform.
b. Upper secondary veins more acute than lower.
c. Divergence angle varies regularly.
d. Spacing (uniform, increasing towards the vein, irregular)

D. **Tertiary (3^o) vein**

1. Venation pattern
a. Opposite percurrent
b. Alternate percurrent
c. Random reticulate
d. Regular polygonal reticulate
e. Forming commissural veins to sinuses
f. Free, ending in sinuses
g. Free and forked, touching margins
2. Secondary vein size: (Weak, moderate, stout, massive)
3. Angle of divergence- ranges of values for the angle of divergence category were showed in Table 2.

4. Variation in angle of divergence.
a. Nearly uniform.
b. Upper 2^o veins more acute than lower.
c. Divergence angle varies regularly.
d. Spacing (uniform, increasing towards the base, irregular)

E. Quaternary vein

Venation pattern: alternate percurrent, opposite percurrent, regular polygonal reticulate

F. Areoles

1. Present/Absent
a. present
b. absent
2. Number of sides
a. 3 sided
b. 4 sided
c. 5 or more sided

G. Freely ending ultimate veins of the leaf (F.E.V.S.)

a. Absent
b. Unbranched
c. 1-branched
d. 2 or more branched

RESULTS AND DISCUSSION

Leaf Architecture Characters of Eupolypods I

General Characteristics of Eupolypods I

Two general leaf architecture characters were examined, namely, morphological characters and venation patterns based on common leaf morphology. Morphological characters included, leaf organization, shape, apex shape, length and width ratio, blade class, base shape, base angle, base symmetry, margin, and lobation. Whereas the latter was parallel with Conda et al. (2017) and Tan and Buot (2019), which included 1° vein, 2° vein, 3° vein, 4° vein, and areoles.

Eupolypods I species exhibited various morphological characters and offered many variable taxonomic characteristics such as simple to quadripinnate leaf organization, lanceolate to oblong shape, nanophyll to macrophyll blade class, entire to serrate margin, and unlobed to lobed leaf (Table 1). This supports the claim of Christenhusz and Chase (2014) that families under this clade are morphologically divergent making it difficult to see the group as one clade. Although a diversity of leaf organization exists throughout eupolypods I, most species have pinnate leaves and this state is exhibited throughout eight species (Table 2).

On the other note, the venation patterns of eupolypods I species were complex which ended up to 4° vein with areoles. Apparently, all representative species exhibited pinnate 1° vein with weak to massive sizes. However, the most conspicuous variation in eupolypods I species involves higher and finer venations: secondary (2°) vein, tertiary (3°) vein, quaternary (4°) vein, and areoles.

Table 1. Summary of the general morphological characters of eupolypods I species.

General Morphological Characters	
Leaf organization	Pinnate-deeply pinnatifid
Shape (pinna/pinnule)	Mostly lanceolate, few linear and elliptic, rarely oblong
Apex shape (pinna/pinnule)	Mostly acute-acuminate, few round, rare obtuse
Base (pinna/pinnule)	

Table 1 contd.

Shape	Usually truncate, few acute and attenuate, rarely convex and rounded
Angle	Acute to obtuse
Symmetry	Mostly asymmetrical, few symmetrical
Blade class	Nanophyll to macrophyll
Margin type	Entire to serrate
Lobation	Mostly unlobed, few shallow to deep
Venation Pattern	
1^o vein	
Category	Pinnate
Size	Weak to massive
2^o vein	
Category	Mostly cladodromous, some craspedodromous and weak brochidodromous
Size	Mostly weak, few moderate
Angle of divergence	Mostly moderate, few narrow and wide, rarely acute
Variation in angle of divergence	Mostly upper 2^o vein more acute than lower, few nearly uniform, rarely varies irregularly
Spacing	Usually irregular, few nearly uniform, rarely increasing towards base
3^o vein	
Category	Regular polygonal, random reticulate, opposite percurrent, cladodromous, forming commissural vein
Size	Weak
Angle of divergence	Mostly moderate, few narrow, rare right angle
Variation in angle of divergence	Nearly uniform, irregular, upper vein more acute than lower
Spacing	Usually increasing towards the base, few irregular and nearly uniform
4^o vein	
Category	Mostly absent, few regular polygonal reticulate, few alternate percurrent
Areoles	Generally absent, rarely present
Number of sides	Mostly none, few 5 or more sides
F.E.V.S.	Mostly none, few 2 branched, rarely 1 branched

Table 2. Leaf architecture characters of 21 selected species of Eupolypods I: General Morphology

Family	Species	Leaf organization	Shape (lamina/pinna)	Apex shape	L:W ratio	Blade class	Base shape	Base angle	Base symmetry	Margin	Location
Davalliaceae	*Davallia hymenophylloides* (Blume) Kuhn	Quadripinnatifid	Lanceolate	Acute	2.1-2.5:1	Macrophyll	Cuneate	Acute	Asymmetrical	Serrate	Deep
	Davallia solida (Forst.) Sw.	Tripinnate	Oblong	Acute	1.2-2.6:1	Mesophyll	Cuneate	Acute	Asymmetrical	Serrate	Shallow
	Davallia repens Khun	Tripinnatifid	Lanceolate	Acute	2.1-2.5	Macrophyll	Cuneate	Acute	Asymmetrical	Serrate	Shallow
Didymochlaenaceae	*Didymochlaena truncatula* (Sw.) J.Sm.	Bipinnate	Oblong	Round	1.8-2.1:1	Mesophyll	Subtruncate	Wide obtuse	Asymmetrical	Undulate	Unlobed
Dryopteridaceae	*Bolbitis heteroclita* (Pr.) Ching in C. Chr.	Pinnate	Oblong	Caudate	3.8-7.0:1	Notophyll	Cuneate	Acute	Symmetrical	Undulate	Shallow
	Polystichum horizontale C. Presl	Tripinnatifid	Ovate	Acute	3.6-4.0:1	Nanophyll	Cuneate	Acute	Asymmetrical	Serrate	Shallow
	Arachniodes amabilis (Blume) Tindale	Tripinnate	Ovate	Acute	2.5-3.2	Microphyll	Cuneate	Acute	Asymmetrical	Serrate	Moderate
Hypodematiaceae	*Hypodematium crenatum* Kuhn & Decken	Tripinnatifid	Ovate	Acuminate	4.5-6.0:1	Microphyll	Truncate	Obtuse	Asymmetrical	Serrate	Deep
Lomariopsidaceae	*Lomariopsis lineata* (Presl.) Holttum	Pinnate	Oblong	Acuminate	4.1-5.8:1	Notophyll	Acute	Acute	Symmetrical	Entire	Unlobed
	Lomariopsis kingii (Copel.) Holttum	Pinnate	Lanceolate	Acuminate	0.8-1.9:1	Macrophyll	Acute	Acute	Symmetrical	Entire	Unlobed
	Cyclopeltis crenata (Fee) C. Chr.	Pinnate	Lanceolate	Acuminate	3.5-5.8:1	Microphyll	Round	Obtuse	Symmetrical	Entire	Unlobed
Nephrolepidaceae	*Nephrolepis cordifolia* (L.) C. Presl	Pinnate	Oblong	Obtuse	2.0-2.5:1	Nanophyll	Truncate	Obtuse	Asymmetrical	Serrate	Shallow
	Nephrolepis biserrata (Sw.) Schott	Pinnate	Linear	Acute	4.0-4.8:1	Microphyll	Truncate	Obtuse	Asymmetrical	Serrate	Shallow
	Nephrolepis falcata (Cav.) C. Chr.	Pinnate	Linear	Acute	4.0-4.4:1	Microphyll	Truncate	Obtuse	Asymmetrical	Entire	Unlobed
Polypodiaceae	*Microsorium heterocarpum* (Blume) Ching	Simple	Lanceolate	Acuminate	3.4-8.4:1	Mesophyll	Attenuate	Acute	Symmetrical	Entire	Unlobed

Tabl 2. contd.

	Microsorium punctatum (L.) Copel.	Simple	Lanceolate	Acute	7.1-13.3:1	Mesophyll	Attenuate	Acute	Symmetrical	Entire	Unlobed
	Phymatosorus scolopendria (Burm.f.)Pic. Serm.	Pinnatifid	Oblong	Acuminate	1.1-2.7:1	Microphyll	Cuneate	Obtuse	Symmetrical	Entire	Deep
Tectariaceae	*Tectaria angulata* (Willd.) Copel	Deeply pinnatifid	Elliptic	Acute	1.4-2.6:1	Macrophyll	Cordate	Wide obtuse	Asymmetrical	Undulate	Palmate lobed
	Tectaria dissecta (G. Forst.) Lellinger	Bipinnatifid	Lanceolate	Acuminate	2.4-3.0:1	Notophyll	Cuneate	Wide obtuse	Symmetrical	Crenate	Deep
	Tectaria hilocarpa (Fee) M.G. Price	Pinnatifid	Oblong	Acute	1.1-4.2:1	Mesophyll	Attenuate	Acute	Symmetrical	Undulate	Deep
Oleandraceae	*Oleandra maquilingensis* Copel.	Pinnate	Lanceolate	Caudate	5.3-8.8:1	Notophyll	Cuneate	Acute	Symmetrical	Entire	Unlobed

Furthermore, a study of Magrini and Scoppola (2010) showed that general morphology, particularly morphometrics can resolve taxonomic problems of *Ophioglossum* species. They found out that shape and the base of the leaf are important diagnostic characters. However, these characters including leaf shape, size and dissection are also prone to ecophysiological factors such as elevation, climate, and location (Kluge and Kessler, 2007, Conda et al., 2017). Thus, general morphology characters are more effective in addressing taxonomic problems if coupled with other stable characters such as leaf venations, as in the study of Sundue and Rothfels (2014), wherein morphological characters including general morphology and leaf venations were used in characterizing eupolypods II ferns.

Describing Eupolypods I species using Leaf Architecture Characters

A number of description and characterization attempts of the families under eupolypods I have included leaf dissection and venation, as seen in the works of Pray (1960), Wagner (1979), Pryer et al. (1995), and Ding et al. (2013). Surprisingly, the detailed leaf architecture characters of the 21 representative species of eupolypods I in Table 3 showed that all species in the study exhibited pinnate 1^{o} vein. On the other hand, higher venations were found diverse among different species, making higher venation character, a good taxonomic marker.

Some species were devoid of tertiary veins such as the species under the families Davalliaceae (*Davallia hymenophylloides, Davallia repens,* and *Davallia solida*), Dryopteridaceae (*Polystichum horizontale* and *Arachniodes amabilis*), Lomariopsidaceae (*Lomariopsis lineata*, *Lomariopsis kingii* and *Cyclopeltis crenata*), Nephrolepidaceae (*Nephrolepis cordifolia, Nephrolepis biserrata,* and *Nephrolepis falcata*), and Oleandraceae (*Oleandra maquilingensis*). Only the species from Polypodiaceae (*Microsorum heterocarpum*, *Microsorum punctatum* and *Phymatosorus scolopendria*) and Tectariaceae (*Tectaria angulata* and *Tectaria hilocarpa*) displayed higher venations until areoles, except for *Tectaria dissecta* with only up to tertiary vein.

About 52% from the overall species exhibited cladodromous secondary venation pattern while five species for craspedodromous and also five species for weak brochidodromous secondary venation. Species having cladodromous secondary veins mostly showed nearly uniform in terms of variation in angle of divergence.

On the other hand, those with craspedodromous secondary veins exhibited diverse variation in angle of divergence but mostly with irregular spacing. Those species having weak brochidodromous secondary vein usually had upper veins more acute than lower veins in terms of variation in angle of divergence. Also, these species have areoles that are five or more sided and two or more branched.

Table 3. Detailed leaf architecture characters of 21 selected Eupolypods I species (AD-Angle of Divergence, VAD -Variation in the Angle of Divergence, F.E.V.S- Freely Ending Ultimate Veins.

TAXA		**PRIMARY VEIN**		**SECONDARY VEIN**					**TERTIARY VEIN**					**QUATERNARY VEIN**	**AREOLATION**		
FAMILY	**SPECIES**	**Category**	**Size**	**Category**	**Size**	**AD**	**VAD**	**Spacing**	**Category**	**Size**	**AD**	**VAD**	**Spacing**	**Category**	**Present/ Absent**	**Sides**	**F.E.V.S.**
Davalliaceae																	
	Davallia hymenophylloides (Blume) Kuhn	Pinnate	Weak	Craspedodromous	Weak	Moderate	Upper vein more acute than lower	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA
	Davallia solida (Forst.) Sw.	Pinnate	Moderate	Craspedodromous	Weak	Narrow	Upper vein more acute than lower	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA
	Davallia repens Khun	Pinnate	Weak	Craspedodromous	Weak	Narrow	Upper vein more obtuse than lower	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA
Didymochlaenaceae	*Didymochlaena truncatula* (Sw.) J.Sm.	Pinnate	Weak	Cladodromous	Weak	Narrow	Irregular	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA
Dryopteridaceae	*Bolbitis heteroclita* (Pr.) Ching in C. Chr.	Pinnate	Stout	Craspedodromous	Moderate	Moderate	Upper vein more acute than lower	Increasing towards the base	Regular polygonal reticulate	Weak	Narrow	Irregular	Irregular	NA	Absent	NA	NA
	Polystichum horizontale C. Presl	Pinnate	Weak	Cladodromous	Weak	Acute	Nearly uniform	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA

	Arachniodes amabilis (Blume) Tindale	Pinnate	Weak	Cladodromous	Weak	Acute	Nearly uniform	Nearly uniform	NA	NA	NA	NA	NA	NA	Absent	NA	NA
Hypodematiaceae	*Hypodematium crenatum* Kuhn & Decken	Pinnate	Moderate	Craspedodromous	Weak	Acute	Nearly uniform	Irregular	Free and forked touching margins	Weak	Narrow	Nearly uniform	Nearly uniform	NA	Absent	NA	NA
Lomariopsidaceae	*Lomariopsis lineata* (Presl.) Holttum	Pinnate	Moderate	Cladodromous	Weak	Wide	Nearly uniform	Nearly uniform	NA	NA	NA	NA	NA	NA	Absent	NA	NA
	Lomariopsis kingii (Copel.) Holttum	Pinnate	Moderate	Cladodromous	Weak	Moderate	Nearly uniform	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA
	Cyclopeltis crenata (Fee) C. Chr.	Pinnate	Moderate	Cladodromous	Weak	wide	Nearly uniform	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA
Nephrolepidaceae	*Nephrolepis cordifolia* (L.) C. Presl	Pinnate	Moderate	Cladodromous	Weak	Moderate	Upper vein more acute than lower	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA
	Nephrolepis biserrata (Sw.) Schott	Pinnate	Moderate	Cladodromous	Weak	Moderate	Upper vein more acute than lower	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA
	Nephrolepis falcata (Cav.) C. Chr.	Pinnate	Moderate	Cladodromous	Weak	Moderate	Upper vein more acute than lower	Irregular	NA	NA	NA	NA	NA	NA	Absent	NA	NA
Polypodiaceae	*Microsorium heterocarpum* (Blume) Ching	Pinnate	Stout	Weak brochidodromous	Moderate	wide	Upper veins more acute than lower	Nearly uniform	Random reticulate	Weak	Moderate	Upper vein more acute than lower	Irregular	Alternate percurrent	Present	5 or more sided	1 Branched
	Microsorium punctatum (L.) Copel.	Pinnate	Stout	Weak brochidodromous	Moderate	wide	Upper veins	Nearly uniform	Opposite percurrent	Weak	Moderate	Irregular	Nearly uniform	Alternate percurrent	Present	5 or more sided	2 or more branched

							more acute than lower										
	Phymatosorus scolopendria (Burm.f.)Pic. Serm.	Pinnate	Stout	Weak brochidodromous	Moderate	wide	Upper veins more acute than lower	Irregular	Formining commissural veins	Weak	Moderate	Nearly uniform	Increasing towards base	Regular polygonal reticulate	Present	5 or more sided	2 or more branched
Tectariaceae	*Tectaria angulata* (Willd.) Copel	Pinnate	Stout	Weak brochidodromous	Moderate	Moderate	Upper veins more acute than lower	Increasing towards the base	regular polygonal reticulate	Weak	Moderate	Irregular	Increasing towards the base	regular polygonal reticulate	Present	5 or more sided	2 or more Branched
	Tectaria dissecta (G. Forst.) Lellinger	Pinnate	Moderate	Weak brochidodromous	Weak	Narrow	Upper veins more acute than lower	Increasing towards the base	Free and forked touching margins	Weak	Narrow	Upper vein more acute than lower	Increasing towards the base	NA	Absent	NA	NA
	Tectaria hilocarpa (Fee) M.G. Price	Pinnate	Stout	Weak brochidodromous	Moderate	Moderate	Nearly unifrom	Increasing towards the base	Opposite percurrent	Weak	Right angle	Irregular	Irregular	Regular polygonal reticulate	Present	5 or more sided	2 Branched
Oleandraceae	*Oleandra maquilingensis* Copel.	Pinnate	Stout	Cladodromous	Weak	Narrow	Nearly uniform	Nearly uniform	NA	NA	NA	NA	NA	NA	Absent	NA	NA

The results showed success in describing and differentiating the leaf architecture of the species, especially through higher venation patterns. Indeed, this confirmed that leaf venations are taxonomically significant characters that can be used to delineate species of eupolypods I.

Similar results were observed from other works such as Conda and Buot (2018) and Tan and Buot (2019) where ferns differentiate starting from the 2° vein, 3° vein, 4° vein, angle of divergences, and areolation. This holds true even in angiosperms in which higher venation patterns differentiate species including the studies of Baltazar and Buot, (2019), Tan and Buot (2018), Torrefiel and Buot, (2017); Jumawan and Buot (2016), Villareal and Buot (2015), and Laraño and Buot (2010). Detailed illustrations and photographs were provided to show the diverse venation patterns of eupolypods I species (Figs.2-22).

Description of Eupolypods I Used in the Study

Dryopteridaceae

***Bolbitis heteroclita* (Pr.) Ching in C. Chr.** (Fig. 2)
Lamina pinnate. Pinna oblong, 13-15.5 cm long, 22-35 cm wide, apex caudate, base cuneate, base angle acute, symmetrical, margin undulate, shallowly lobed, 3.8-7.0:1 length: width ratio, notophyll.

1^{o} vein pinnate, stout. 2^{o} vein craspedodromous, moderate, angle of divergence moderate, variation in angle of divergence upper 2^{o} vein more acute than lower, spacing increasing towards base. 3^{o} vein regular polygonal reticulate, weak, angle of divergence narrow, variation in angle of divergence inconsistent, spacing irregular. Areoles absent. Exsiccatae: G.E. Edano 3909 (PNH), J.F. Barcelona 190077 (PNH), J.F. Barcelona and J. R. Cabalquinto 190196 (PNH), J. M. Tan 6749 (PBDH)

Fig. 2. *Bolbitis heteroclita* (Pr.) Ching in C. Chr.

Polystichum horizontale **C. Presl** (Fig. 3)

Lamina tripinnatifid. Pinna lanceolate, 12-18 cm long, 2-3 cm width. Pinnule ovate, 1.6-2.2 cm long, 0.4-0.6 cm wide, apex acute, base cuneate, base angle acute, asymmetrical, margin serrate, shallowly lobed, 3.6-4.0:1 length: width ratio, nanophyll.

1^{o} vein pinnate, weak. 2^{o} vein cladodromous, weak, angle of divergence narrow, variation in angle of divergence irregular, spacing irregular. Areoles absent.
Exsiccatae: M.G. Price 14099 (CAHUP), N.M. Orlido 13878 (CAHUP), D.B. Tolentino 41866 (CAHUP), J. M. Tan 6948 (PBDH).

Fig. 3. *Polystichum horizontale* C. Presl.

***Arachniodes amabilis* (Blume) Tindale** (Fig.4)

Lamina tripinnate. Pinna subtriangular, 13.5-25 cm long, 5-9 cm wide. Pinnule ovate, 1.5-2.5 cm long, 0.6-1 cm wide, apex acute, base cuneate, base angle acute, asymmetrical, margin serrate, moderately lobed, 2.5-3.2:1 length: width ratio, microphyll.

1° vein pinnate, weak. 2° vein cladodromous, weak, angle divergence acute, variation in angle of divergence nearly uniform, spacing nearly uniform. Areoles absent.
Exsiccatae: J. Sinclair and G.E. Edano 55240 (PNH), D.R. Mendoza 17227 (PNH), M.G. Price 154950 (PNH), J. Sinclair and G.E. Edano 55240 (PNH), J.M. Tan 6973 (PBDH)

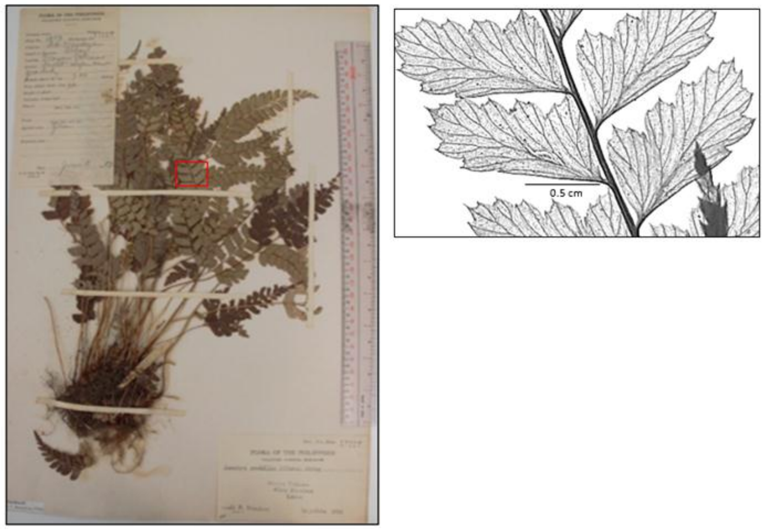

Fig. 4. *Arachniodes amabilis* (Blume) Tindale

Hypodematiaceae

***Hypodematium crenatum* Kuhn & Decken**
(Fig. 5)

Lamina tripinnatifid. Pinna oblong, 18-33 cm long, 4-9 cm wide. Pinnule ovate, 5.5-9 cm long, 1.2-1.5 cm wide, apex acuminate, base truncate, base angle obtuse, asymmetrical, margin serrate, deeply lobation, 4.5-6.0:1 length: width ratio, microphyll.

1° vein pinnate, moderate. 2° vein craspedodromous, weak, angle of divergence acute, variation in angle of divergence nearly uniform, spacing upper veins more acute than base, 3° vein cladodromous, weak, angle of divergence narrow, variation in angle of divergence nearly uniform, spacing irregular. Areoles absent.
Exsiccatae: L. Co 9805 (PUH), J.M. Tan 6978 (PBDH), J.M. Tan 6979 (PBDH)

Fig. 5. *Hypodematium crenatum* Kuhn & Decken

Tectariaceae

***Tectaria angulata* (Willd.) Copel** (Fig. 6)

Lamina deeply pinnatifid, 23-38 cm long, 10-18 cm wide, elliptic, apex acute, base shape cordate, base angle wide obtuse, asymmetrical, margin undulate, palmately lobed, 1.4-2.6:1 length: width ratio, macrophyll.

1^{o} vein pinnate, stout. 2^{o} vein weak brochidodromous, moderate, angle of divergence moderate, variation in angle of divergence upper 2^{o} vein more obtuse than lower, spacing increasing towards the base, 3^{o} vein regular polygonal reticulate, weak, angle of divergence moderate, variation in angle of divergence irregular, spacing increasing towards the base. 4^{o} vein regular polygonal reticulate. Areoles present, 5 or more sided, 2 or more branched.
Exsiccatae: H.H. Bartlett 56942 (PNH), R.B. Fox 3943 (PNH), A.D.E. Elmer 196680 (PNH), J. F. Barcelona, N.E. Dolotina, G.S. Madronero and D.D. Sapot 199152 (PNH), J.M. Tan 6994 (PBDH)

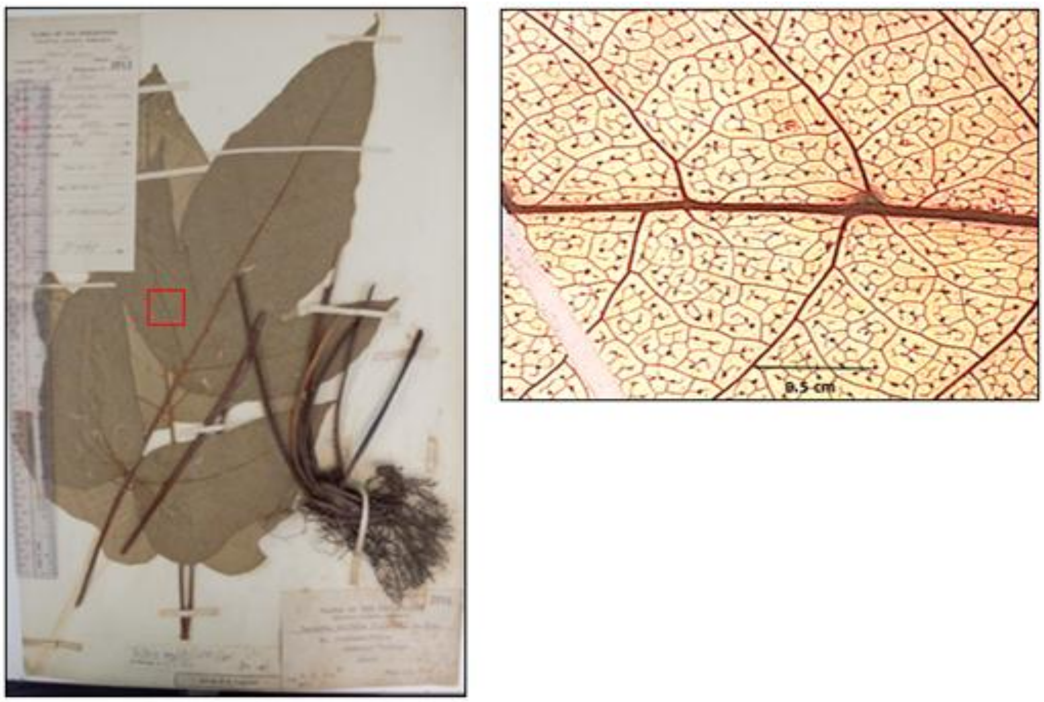

Fig. 6. *Tectaria angulata* (Willd.) Copel

***Tectaria dissecta* (G. Forst.) Lellinger** (Fig. 7)

Lamina bipinnatifid. Pinna lanceolate, 12-18 cm long, 5-6 cm wide, apex acuminate, base cuneate, base angle wide obtuse, symmetrical, margin crenate, deeply lobed, 2.4-3.0:1 length: width ratio, notophyll.

1^{o} vein pinnate, moderate. 2^{o} vein craspedodromous, weak, angle of divergence moderate, variation in angle of divergence upper 2^{o} vein more acute than lower, spacing increasing towards the base. 3^{o} vein cladodromous, weak, angle of divergence narrow, variation in angle of divergence upper 3^{o} vein more acute than lower, spacing increasing towards the base. Areoles absent.

Exsiccatae: Iwatsuki, Murata, Guttierrez 126012 (PNH), G.E. Edano 41283 (PNH), M.G. Price 155147 (PNH), G.E. Edano 16585 (PNH), J.M. Tan 6997 (PBDH)

***Tectaria hilocarpa* (Fee) M.G. Price** (Fig. 8)

Lamina pinnatifid, 15-21 cm long, 4-14 cm wide, oblong, apex acute, base attenuate, base angle acute, symmetrical, margin undulate, deeply lobed, 1.1-4.2:1 length: width ratio, mesophyll.
1^{o} vein pinnate, stout. 2^{o} vein weak brochidodromous, moderate, angle of divergence wide, variation in angle of divergence nearly uniform, spacing increasing towards the base. 3^{o} vein opposite percurrent, weak, angle of divergence right angle, variation in angle of

divergence irregular, spacing irregular. 4^{o} vein regular polygonal reticulate, areoles present, 5 or more sided, 2 branched. Exsiccatae: J.M.Tan 6992 (PBDH), J.M.Tan 6993 (PBDH)

Fig. 7. *Tectaria dissecta* (G. Forst.) Lellinger

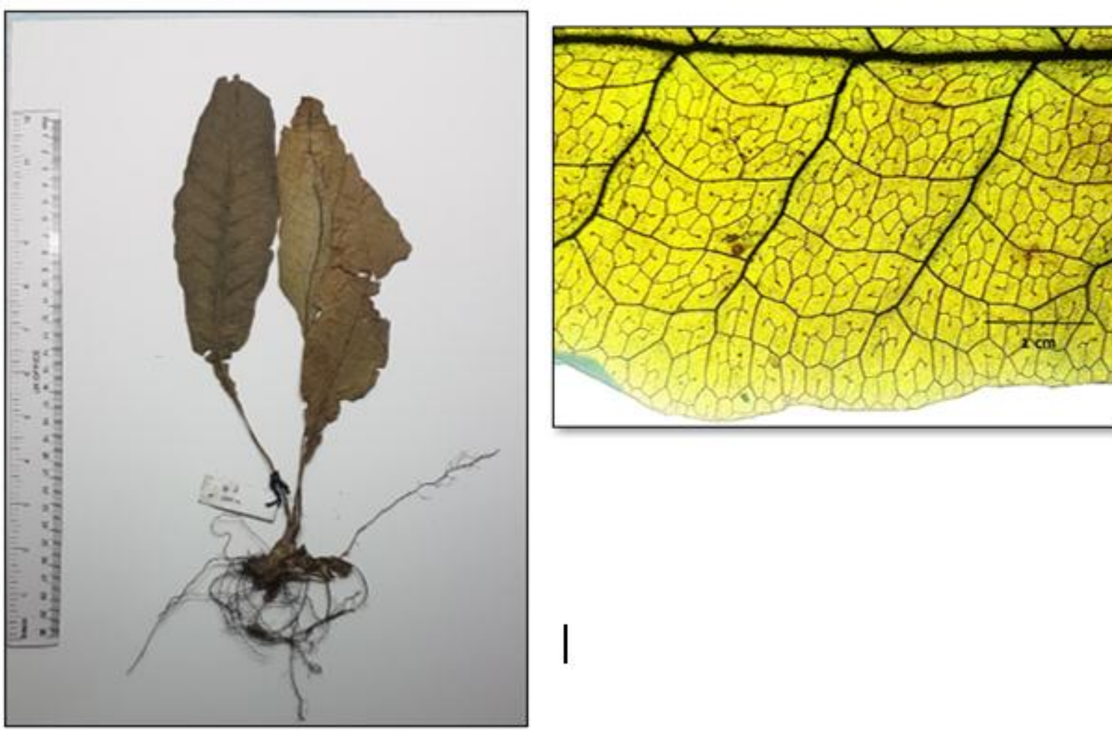

Fig. 8. *Tectaria hilocarpa* (Fee) M.G. Price

Oleandraceae

***Oleandra maquilingensis* Copel.** (Fig. 9)

Lamina pinnate, 16-22.5 cm long, 2-2.5 cm wide, lanceolate, apex caudate, base cuneate, base angle acute, symmetrical, margin entire, 5.3-8.8:1 length: width ratio, notophyll.

1^{o} vein pinnate, stout. 2^{o} vein cladodromous, weak, angle of divergence narrow, variation in angle of divergence nearly uniform, spacing nearly uniform, areoles absent.
Exsiccatae: M.C.N. Banaticla 3346 (PBDH), E.B. Copeland 199230 (PNH), A.D. Elmer 197457 (PNH), J.M. Tan 6976 (PBDH)

Fig. 9. *Oleandra maquilingensis* Copel.

Davalliaceae
***Davallia hymenophylloides* (Blume) Kuhn** (Fig. 10)
Lamina quadripinnatifid. Pinnae linear-triangular, 13-18 cm long, 3-9cm wide, linear-triangular. Pinnule lanceolate, 25-28 cm long, 10-13 cm wide, apex acute, base cuneate, base angle acute, asymmetrical, margin serrate, deeply lobed, 2.1-2.5:1 length: width ratio, macrophyll.

1^{o} vein pinnate, weak. 2^{o} vein cladodromous, weak, angle of divergence moderate, upper 2^{o} vein more acute than lower, irregularly spaced. Areoles absent.
Exsiccatae: M.C.N. Banaticla 3358 (PBDH), M.D. Sulit 20295 (PNH), J.F. Barcelona 190108 (PNH), M.D. Sulit 20272 (PNH), J.M. Tan 6938 (PBDH)

Fig. 10. *Davallia hymenophylloides* (Blume) Kuhn

Davallia solida **(Forst.) Sw.** (Fig. 11)

Lamina tripinnate. Pinnae subtriangular, 11-28 cm long, 6-15 cm wide. Pinnule oblong, 4-10 cm long, 1.5-8 cm wide, apex acute, base cuneate, base angle acute, asymmetrical, margin serrate, shallowly lobed, 1.2-2.6:1 length: width ratio, mesophyll.

1^{o} vein pinnate, moderate. 2^{o} vein craspedodromous, weak, narrow, upper 2^{o} vein more obtuse than lower, irregularly spaced. Areoles absent.

Exsiccatae: E. Reynoso 168693 (PNH), J. Barcelona 190274 (PNH), J. Barcelona 190251 (PNH), M.G. Price 160888 (PNH), J.M. Tan 6942 (PBDH)

Fig.11. *Davallia solida* (Forst.) Sw.

Davallia repens **Khun** (Fig. 12)

Lamina tripinnatifid. Pinna subtriangular, 3.5-5.5 cm long, 1.5-2.5 cm wide. Pinnule lanceolate, 1.5-2.5 cm long, 1-1.2 cm wide, apex acute, base cuneate, base angle acute, asymmetrical, margin serrate, shallowly lobed, 2.1-2.5:1 length: width ratio, macrophyll.

1^{o} vein pinnate, weak. 2^{o} vein craspedodromous, weak, angle of divergence narrow, variation in angle of divergence irregular, spacing irregular. Areoles absent.

Exsiccatae: J.M.Tan 6940 (PBDH), J.M. Tan 6941 (PBDH)

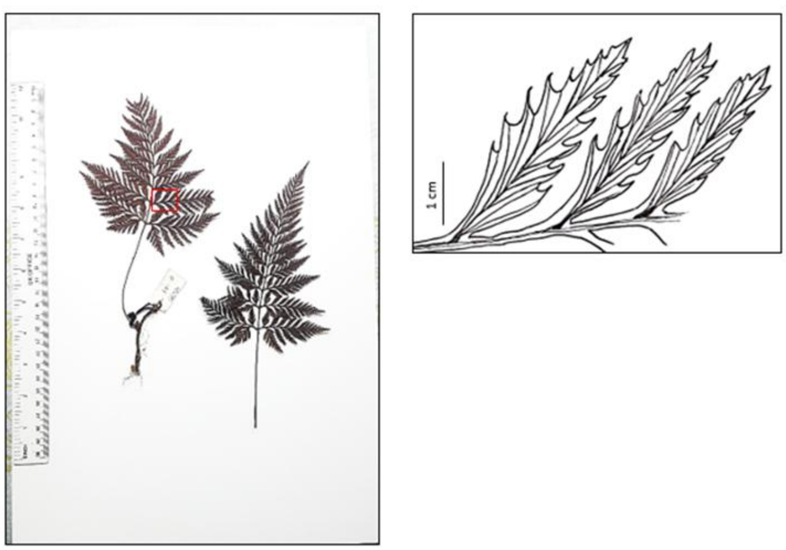

Fig 12. *Davallia repens* Khun

Didymochlaenaceae

***Didymochlaena truncatula* (Sw.) J.Sm.** (Fig. 13)

Lamina bipinnate. Pinna linear, 18 -25 cm long, 2-4 cm wide. Pinnule oblong, 1.3-1.7 cm long to 0.7-0.8 cm wide, apex round, base subtruncate, base angle wide obtuse, asymmetrical, undulate, unlobed, 1.8-2.1:1 length: width ratio, mesophyll.

1° vein pinnate, weak. 2° vein cladodromous, weak, angle of divergence narrow, variation of angle of divergence irregular, spacing irregular. Areoles absent.

Exsiccatae: B. Hernaez 1456 (PNH), Gutierrez, Yen and Reynoso 108981 (PNH), G.E. Edano 11222 (PNH), D.R. Mendoza and P. Convocar 8706 (PNH)

Fig. 13. *Didymochlaena truncatula* (Sw.) J.Sm**.**

Lomariopsidaceae

***Lomariopsis lineata* (Presl.) Holttum** (Fig. 14)

Lamina pinnate. Pinna oblong, 13-17.5 cm long, 3-4 cm wide, apex acuminate, base acute, base angle acute, symmetrical, margin entire, unlobed, 4.1-5.8:1 length: width ratio, notophyll.

1° vein pinnate, moderate. 2° vein cladodromous, weak, angle of divergence wide, variation in angle of divergence nearly uniform, spacing nearly uniform. Areoles absent.

Exsiccatae: M.G. Price 22730 (CAHUP), M.G. Price 22729 (CAHUP), M.G. Price 15162 (CAHUP), San Juan and Vendiril 126046 (PNH), A.D.E. Elmer 197315 (PNH).

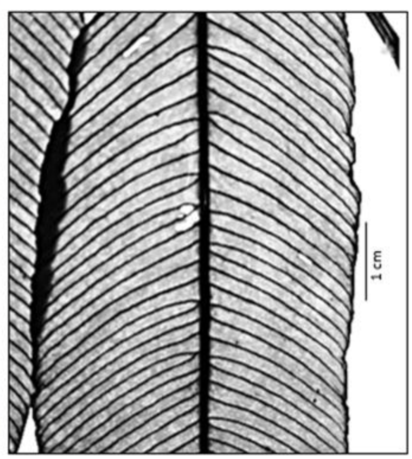

Fig. 14. *Lomariopsis lineata* (Presl.) Holttum

***Lomariopsis kingii* (Copel.) Holttum** (Fig. 15)

Lamina pinnate. Pinna lanceolate, 23.5-16.3 cm long, 12-20 cm wide, apex acuminate, base acute, base angle acute, symmetrical, margin entire, unlobed, 0.8-1.9:1 length: width ratio, macrophyll.

1^{o} vein pinnate, moderate. 2^{o} vein cladodromous, weak, angle of divergence moderate, variation in angle of divergence nearly uniform, spacing irregular, areoles absent.

Exsiccatae: H.C. Conklin 17252 (PNH), J.M.Tan 6991 (PBDH)

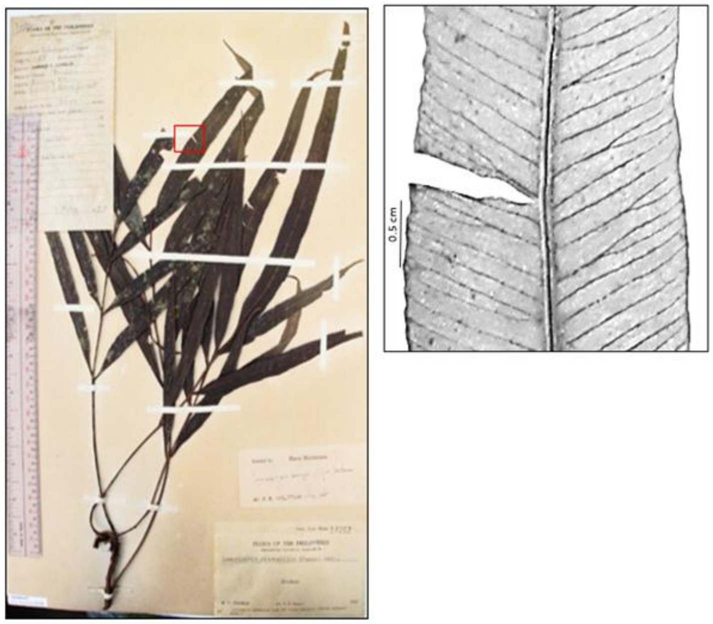

Fig. 15. *Lomariopsis kingii* (Copel.) Holttum

***Cyclopeltis crenata* (Fee) C. Chr.** (Fig. 16)

Lamina pinnate. Pinna lanceolate, 6-10 cm long, 1.4-1.8 cm wide, apex acuminate, base round, base angle, obtuse, symmetrical, margin entire, unlobed, 3.5-5.8:1 length: width ratio, microphyll.

1^{o} vein pinnate, moderate. 2^{o} vein cladodromous, weak, angle of divergence wide, variation in angle of divergence nearly uniform, spacing irregular. Areoles absent.

Exsiccatae: F.A. McClure 26645 (PNH), F.A. McClure 62998 (PNH), F.A. McClure 62998 (PNH), J.M. Tan 6988 (PBDH)

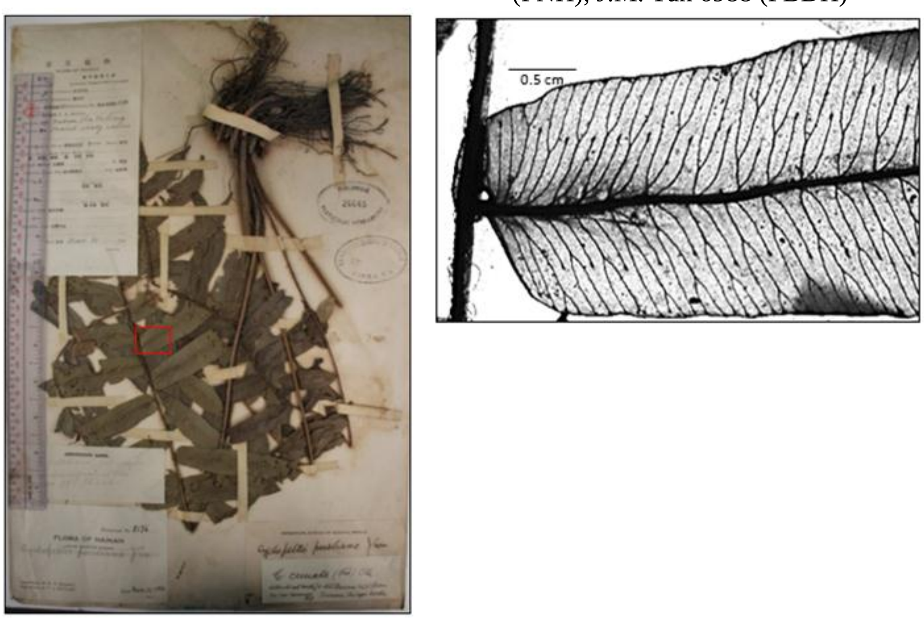

Fig 16. *Cyclopeltis crenata* (Fee) C. Chr.

Nephrolepidaceae

***Nephrolepis cordifolia* (L.) C. Presl** (Fig. 17)

Lamina pinnate. Pinna oblong, 1.5-2.5 cm long, 0.6-1.2 cm wide, apex obtuse, base truncate, base angle obtuse, asymmetrical, crenate, shallowly lobed, 2.0-2.5:1 length: width ratio, nanophyll.

1^{o} vein pinnate, moderate. 2^{o} vein cladodromous, weak, angle of divergence moderate, variation in angle of divergence upper vein more acute than lower, spacing irregular. Areoles absent.
Exsiccatae: M.C.N. Banaticla 3288 (PBDH), M. delos Angeles 6176 (PBDH), D.E. Elmer 56541 (PNH), J.M. Tan 6944 (PBDH)

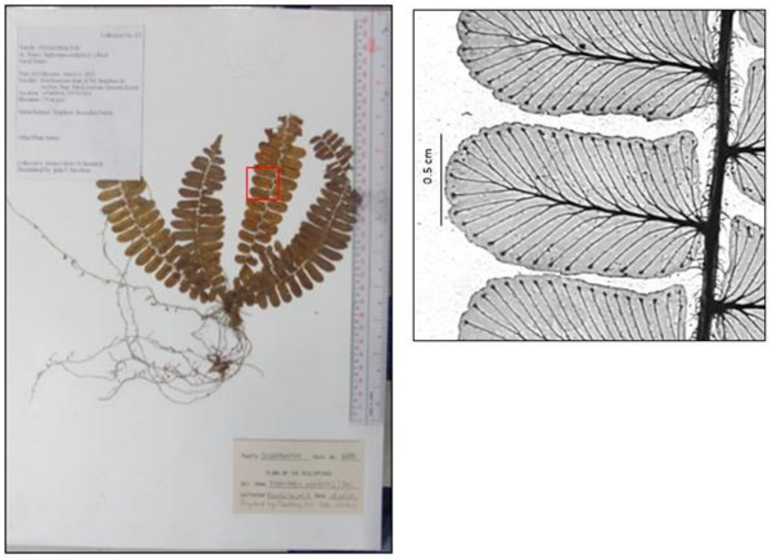

Fig 17. *Nephrolepis cordifolia* (L.) C. Presl

***Nephrolepis biserrata* (Sw.) Schott** (Fig. 18)

Lamina pinnate. Pinna linear, 6-12 cm long, 1.5-2.5 cm wide, apex acute, base truncate, base angle obtuse, asymmetrical, margin serrate, shallowly lobed, 4.0-4.8:1 length: width ratio, microphyll.
1^{o} vein pinnate, moderate. 2^{o} vein cladodromous, weak, angle of divergence moderate, variation in angle of divergence upper vein more acute than lower, spacing irregular. Areoles absent.
Exsiccatae: M.L. Steiner 39547 (PNH), A. Castro 5882 (PNH), E. Quisumbing, R. Del Rosario, H. Guttierrez 79497 (PNH), E. Quisumbing, R. Del Rosario, H. Guttierrez 79462 (PNH), M.D. Sulit 4523 (PNH)

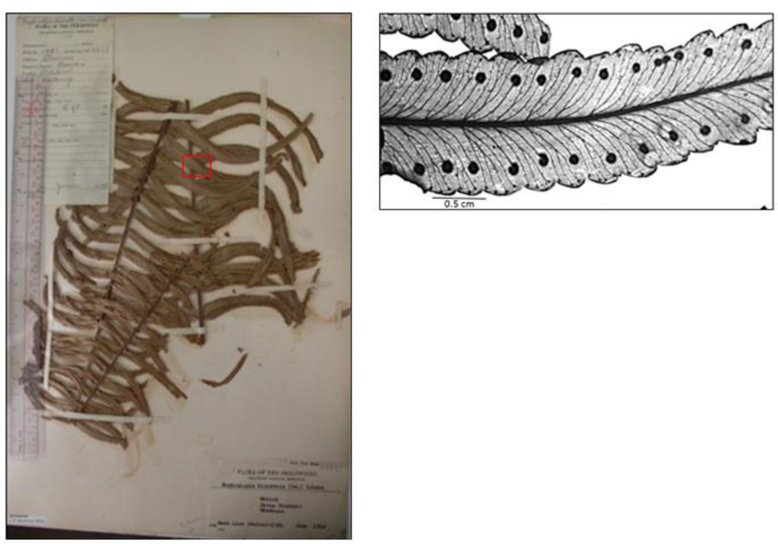

Fig 18. *Nephrolepis biserrata* (Sw.) Schott

***Nephrolepis falcata* (Cav.) C. Chr.** (Fig. 19)

Lamina pinnate. Pinna linear, 5-5.3 cm long, 1-1.3 cm wide, apex acute, base truncate, base angle obtuse, asymmetrical, margin entire, unlobed, 4.0-4.4:1 length: width ratio, microphyll.

1^{o} vein pinnate, moderate. 2^{o} vein cladodromous, weak, angle of divergence moderate, variation in angle of divergence upper vein more acute than lower, spacing irregular. Areoles absent.

Exsiccatae: A.D. Elmer 196498 (PNH), Y. Kondo and G. Edano 38676 (PNH), J.F. Barcelona 190176 (PNH), J.F. Barcelona 190167 (PNH), G.E. Edano 11170 (PNH)

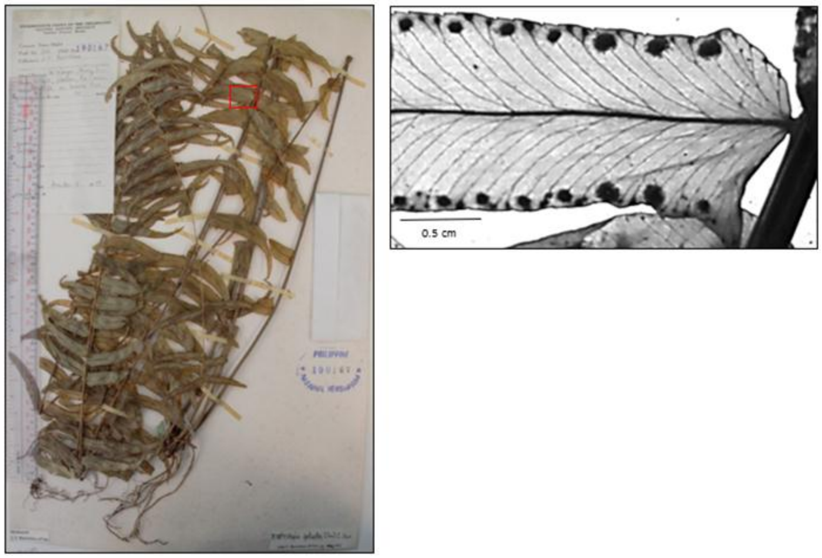

Fig 19. *Nephrolepis falcata* (Cav.) C. Chr.

Polypodiaceae

***Microsorium heterocarpum* (Blume) Ching** (Fig.20)

Lamina simple, 21-30 cm long, 2-10 cm wide, lanceolate, apex acuminate, base attenuate, base angle acute, symmetrical, margin entire, unlobed, 3.4-8.4:1 length: width ratio, mesophyll.

1^{o} vein pinnate, stout. 2^{o} vein weak brochidodromous, moderate, angle of divergence wide, variation in angle of divergence upper 2^{o} vein more acute than lower, spacing nearly uniform. 3^{o} vein random reticulate, weak, angle of variation moderate, variation in angle of divergence upper 3^{o} vein more acute than lower, spacing irregular. 4^{o} vein alternate percurrent, areoles present, 5 or more sided, 1 branched.

Exsiccatae: B.S. Parris 26202 (CAHUP), L. Co 14961 (PUH), L. Co 13144 (PUH), L.Co 12373 (PUH)

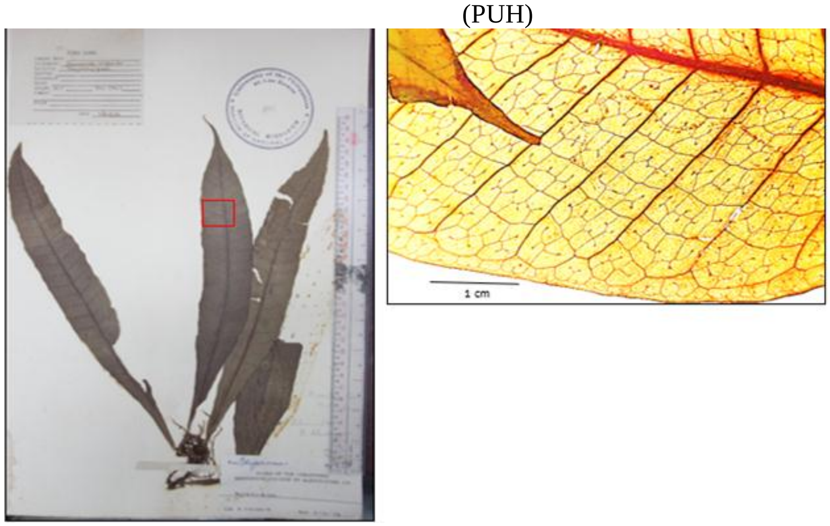

Fig. 20. *Microsorium heterocarpum* (Blume) Ching

***Microsorium punctatum* (L.) Copel.** (Fig.21)

Lamina simple, 23.5-60 cm long, 4.5-7 cm wide, lanceolate, apex acute, base attenuate, base angle acute, symmetrical, margin entire, unlobed, 7.1-13.3:1 length: width ratio, mesophyll.

1^o vein pinnate, stout. 2^o vein weak brochidodromous, moderate, angle of divergence wide, variation in angle of divergence upper 2^o veins more acute than base, spacing nearly uniform. 3^o vein opposite percurrent, weak, angle of divergence moderate, variation in angle of divergence inconsistent, spacing nearly uniform, 4^o vein alternate percurrent, areoles present, 5 or more sided, 2 or more branched.

Exsiccatae: B.F. Hernaez and M.A. Cajano 56116 (CAHUP), B.F. Hernaez and M.A. Cajano 56118 (CAHUP), G. Germar 19954 (PUH), L. Co 2491 PUH 13964

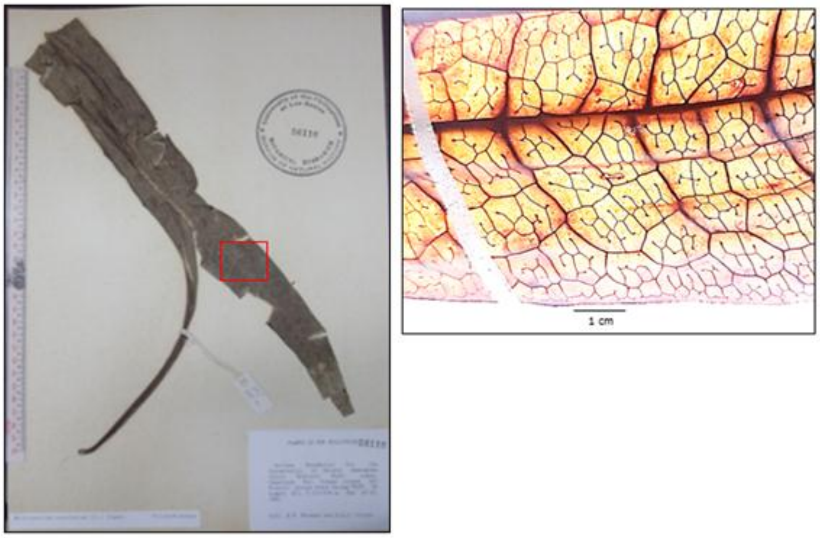

Fig. 21. *Microsorium punctatum* (L.) Copel

***Phymatosorus scolopendria* (Burm.f.) Pic. Serm.** (Fig.22)

Lamina pinnatifid, oblong, apex acuminate, base cuneate, base angle obtuse, symmetrical, margin entire, deeply lobed, 1.1-2.7:1 length: width ratio, microphyll.

1^o vein pinnate, massive. 2^o vein craspedodromous, moderate, angle of divergence moderate, variation in angle of divergence nearly uniform, spacing irregular. 3^o vein forming commissural veins, weak, angle of divergence moderate, variation in angle of divergence nearly uniform, spacing increasing towards the base. 4^o vein regular polygonal reticulate, areoles present, 5 or more sided, 2 or more branched.

Exsiccatae: J.M. Tan 6980 (PBDH), J.M. Tan 6981 (PBDH), M. delos Angeles 6934 (PBDH), M. delos Angeles 6935 (PBDH)

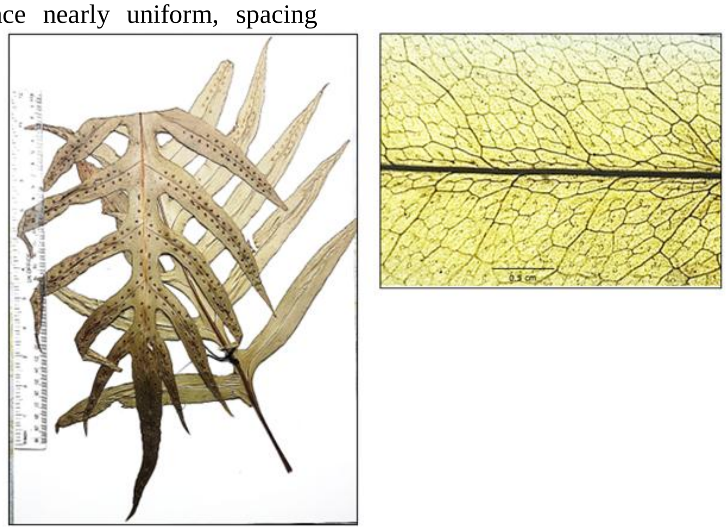

Fig. 22. *Phymatosorus scolopendria* (Burm.f.) Pic. Serm.

Key to the selected species of Eupolypods I based on leaf architecture characters

1 3^o vein present
2 Areoles absent
3 Regular polygonal reticulate 3^o vein ------------------------*Bolbitis heteroclita*
3 Free and forked not polygonal margin 3^o vein
4 Nearly uniform VAD------------------------------*Hypodematium crenatum*
4 Upper 2^o vein more acute than lower VAD----------------*Tectaria dissecta*
2 Areoles present
5 3^o vein AD right angle---*Tectaria hilocarpa*
5 3^o vein AD moderate
6 1 branched areoles---------------------------------*Microsorum heterocarpum*
6 2 or more branched areoles
7 4^o vein alternate percurrent----------------------*Microsorum punctatum*
7 4^o vein regular polygonal reticulate
8 Nearly uniform 3^o AD------------------*Phymatosorus scolopendria*
8 Irregular 3^o AD------------------------------------*Tectaria angulata*

1 3^o vein absent
9 2^o vein nearly uniform spacing
10 1^o vein weak---*Arachniodes amabilis*
10 1^o vein moderate
11 2^o vein AD narrow-----------------------------------*Oleandra maquilingensis*
11 2^o vein AD wide---*Lomariopsis lineata*
9 2^o vein irregular spacing
12 Craspedodromous 2^o vein
13 2^o vein AD moderate --------------------------- *Davallia hymenophylloides*
13 2^o vein AD narrow
14 VAD upper 2^o vein more acute than lower----------------------------- *Davallia solida*
14 VAD upper 2^o vein More obtuse than lower----------------------------*Davallia repens*
12 Cladodromous
15 Linear shape
16 Serrate margin---*Nephrolepis biserrata*
16 Entire margin--*Nephrolepis falcata*
15 Lanceolate shape
17 Macrophyll---*Lomariopsis kingii*
17 Microphyll--- *Cyclopeltis crenata*
16 Oblong shape
18 Apex obtuse--*Nephrolepis cordifolia*
18 Apex round--------------------------------------*Didymochlaena truncatula*
16 Ovate shape---*Polystichum horizontale*

CONCLUSION

Eupolypods I can be described using leaf architecture characters. Venation characters, such as 2^o vein, 3^o vein, 4^o vein, vein size, angle of divergence, variation in angle of divergence, vein spacing, areoles, and F.E.V.S. were found to be useful characters in identifying and describing eupolypods I species, and possibly other fern genera. A dichotomous key illustrated the practical use of leaf architecture characters in identifying and describing eupolypods I.

The study showed the significance of leaf architecture character as a stable taxonomic character confining the findings of Roth-Nebelsick et al. (2001) that it is genetically fixed.

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