ความสัมพันธ์ด้านวิวัฒนาการชาติพันธุ์และฟีนิติกของเฟิร์นสกุล *Lepisorus* (J. SMITH) CHING (POLYPODIACEAE) และสกุลใกล้เคียง

นายวรรณชัย ชาแท่น

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
สาขาวิชาวิทยาศาสตร์ชีวภาพ
คณะวิทยาศาสตร์ จุฬาลงกรมหาวิทยาลัย
ปีการศึกษา 2550

PHYLOGENETIC AND PHENETIC RELATIONSHIPS OF THE FERN GENUS *Lepisorus* (J. SMITH) CHING (POLYPODIACEAE) AND RELATED GENERA

Mr. Wannachai Chatan

A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy Program in Biological Sciences

Faculty of Science
Chulalongkorn University

Academic Year 2007

Thesis Title	PHYLOGENETIC AND PHENETIC RELATIONSHIPS OF THE FERN GENUS *Lepisorus* (J. SMITH) CHING (POLYPODIACEAE) AND RELATED GENERA
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Field of Study	Biological Sciences
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วรรณชัย ชาแท่น : ความสัมพันธ์ด้านวิวัฒนาการชาติพันธุ์และฟีนิติกของเฟิร์นสกุล *Lepisorus* (J.SMITH) CHING (POLYPODIACEAE) และสกุลใกล้เคียง. (PHYLOGENETIC AND PHENETIC RELATIONSHIPS OF THE FERN GENUS *Lepisorus* (J. SMITH) CHING (POLYPODIACEAE) AND RELATED GENERA) อ.ที่ปรึกษา: ศ.ดร. ทวีศักดิ์ บุญเกิด, อ.ปรึกษาร่วม: Bernard R. Baum, Ph.D., 102 หน้า.

Lepisorus (J. Smith) Ching s.l. เป็นเฟิร์นสกุลหนึ่งซึ่งส่วนใหญ่มีการกระจายพันธุ์ในเขตโลกเก่า ปัจจุบันการกำหนดขอบเขตทางอนุกรมวิธานของเฟิร์นสกุลนี้ยังไม่ชัดเจน เนื่องจากบางครั้งได้รวมเฟิร์นสกุลใกล้เคียงคือสกุล *Paragramma* และ *Platygyria* ไว้ด้วย และบางครั้งสกุล *Platygyria* ถูกนำไปรวมกับสกุล *Neocheiropteris* ดังนั้นวัตถุประสงค์หลักของงานวิจัยนี้คือเพื่อกำหนดขอบเขตทางอนุกรมวิธานของเฟิร์นสกุล *Lepisorus*, *Paragramma* และ *Platygyria* ในด้านฟีนิติกได้ใช้การวิเคราะห์การจัดกลุ่มและการวิเคราะห์จัดจำแนกโดยใช้ลักษณะทางสันฐานวิทยาและกายวิภาคศาสตร์จำนวน 53 ลักษณะ และในการวิเคราะห์ด้านวิวัฒนาการชาติพันธุ์ได้ใช้ลักษณะทางสันฐานวิทยาและกายวิภาคศาสตร์จำนวน 33 ลักษณะ ผลการศึกษาที่ได้จากทั้งการวิเคราะห์จัดกลุ่มและการวิเคราะห์จัดจำแนก ได้แยกตัวอย่างพันธุ์ไม้ทั้งหมดออกเป็น 3 กลุ่มคือกลุ่มที่ 1 เป็นตัวอย่างของเฟิร์นสกุล *Neocheiropteris ensata* และ *N. palmatopedata* กลุ่ม 2 เป็นของเฟิร์นสกุล *Platygyria* และกลุ่มที่ 3 เป็นตัวอย่างพรรณไม้ของเฟิร์นสกุล *Lepisorus* s.s., *Neocheiropteris normalis* และสกุล *Paragramma* จากผลการศึกษาด้านฟีนิติกสรุปได้ว่าควรจำแนกเฟิร์นสกุล *Platygyria* ออกจากสกุลอื่น ควรรวมสกุล *N. normalis* และ *Paragramma* ไว้ในสกุล *Lepisorus* และควรแยกเฟิร์นสกุล *Neocheiropteris* ที่เหลือออกเป็นสกุลต่างหาก ผลการวิเคราะห์ความสัมพันธ์ด้านวิวัฒนาการชาติพันธุ์โดยใช้ลักษณะดังกล่าว ไม่สามารถประเมินการกำหนดขอบเขตของเฟิร์นสกุลดังกล่าวได้ เนื่องจาก clade ส่วนใหญ่บน tree มีค่า bootstrap support ต่ำกว่า 50% ดังนั้นจากผลการศึกษาทั้งหมดจึงสรุปว่า ควรแยกสกุล *Platygyria* ออกจากสกุลอื่นๆ ขอบเขตของสกุล *Lepisorus* ควรรวม *N. normalis* และ *Paragramma* และควรแยกเฟิร์นสกุล *Neocheiropteris* ที่เหลือออกเป็นสกุลต่างหากตามผลการศึกษาความสัมพันธ์ด้านฟีนิติก

สาขาวิชา...วิทยาศาสตร์ชีวภาพ.........ลายมือชื่อนิสิต...

ปีการศึกษา.........2550.....................ลายมือชื่ออาจารย์ที่ปรึกษา.................................

ลายมือชื่ออาจารย์ที่ปรึกษาร่วม.................................

4673825123 : BIOLOGICAL SCIENCES

KEYWORD: *Lepisorus* / *Paragramma* / *Platygyria* / MULTIVARIATE ANALYSIS/ PHYLOGENETIC ANALYSIS

WANNACHAI CHATAN: PHYLOGENETIC AND PHENETIC RELATIONSHIPS OF THE FERN GENUS *Lepisorus* (J. SMITH) CHING (POLYPODIACEAE) AND RELATED GENERA
THESIS ADVISOR : PROF. THAWEESAKDI BOONKERD, Ph.D., THESIS COADVISOR : BERNARD R. BAUM, Ph.D., 102 pp.

Lepisorus (J. Sm.) Ching s.l. is a fern genus that mostly occurs in the Old World. So far its taxonomic circumscription remains unclear because sometimes it included or excluded its related taxa, i.e. *Paragramma* and *Platygyria*, and sometimes *Platygyria* was merged to the genus *Neocheiropteris*. This research mainly aims to clarify the circumscriptions of the genus *Lepisorus*, *Paragramma* and *Platygyria*. In the phenetic approach, cluster and discriminant analyses have been performed based on 53 morphological and anatomical characters and the evolutionary approach a phylogenetic analysis was carried out based on 33 morphological and anatomical characters. The result from both cluster and canonical discriminant analyses showed that the specimens were separated into three groups: (1) specimens of *Neocheiropteris ensata* and *N. palmatopedta*, (2) specimens of *Platygyria* (3) specimens of *Lepisorus* s.s., *Neocheiropteris normalis and Paragramma.* Therefore based on phenetic analyses, the *Platygyria* should be treated as distinct taxon, and *N. normalis* and *Paragramma* should be merged with the genus *Lepisorus*. In addition, the *Neocheiropteris* should be treated as a distinct genus. In the phylogenetic approach, the result cannot be used for the circumscriptions of these genera because most clades on were poorly supported by bootstrap analysis. Therefore, the *Platygyri*a should be treated as a distinct genus while the circumscription of the *Lepisorus* should include *N. normalis* and *Paragramma* and the rest of *Neocheiropteris* should be treated as a distinct genus in accordance with the results obtained from phenetic analyses.

Field of study……Biological Sciences…..Student's signature…Wannachai C.……………
Acadermic year…………2007…………..Advisor's signature…Thaweesakdi Boonkerd
Coadvisor's signature…R. Baum…………………

ACKNOWLEDGEMENTS

I would like to express my deepest thanks to my advisor, Professor Dr. Thaweesakdi Boonkerd and my co-advisor, Dr. Bernard R. Baum for their encouragement and valuable advice which had a great benefit through my thesis work.

I also would like to express my sincere thanks to the thesis committee, Associate Professor Dr. Preeda Boon-Long, Associate Professor Dr. Kumthorn Thirakhupt, Assistant Professor Dr. Chumpol Khunwasi, and Associate Professor Dr. Kitichate Sridith for their valuable suggestions.

I am grateful to the curators or keepers of the following herbaria: BKF, BM, E, K, KUN, L, PYU, who allowed access and facilitated the study of the herbarium specimens. Many thanks are due to Dr. M.C. Roos (L), Dr. Liu Ende (KUN), Dr. Xiangjingying (KUN), Prof. S.K. Wu (KUN), Dr. Zhao-Rong He (PYU), Dr. David J. Middleton (E), Dr. P. Hovenkamp (L), Dr. H.P. Nooteboom (L), Dr. M.J. Zink, Miss Suchada Wongpakam and TwinNuch-Nui for their help or suggestions or for supplying the literatures, and the curator or keeper of TI, who gave some type-specimen images to him. I appreciate for the research facilities at Department of Botany, Faculty of Science, Chulalonkorn University.

I am grateful to the many Thai students in the Netherlands, for their assistance during my visit to Leiden. This project was partially supported by the Thai government budget 2006, under the Research Program on Conservation and Utilization of Biodiversity and the Center of Excellence in Biodiversity, Faculty of Science, Chulalongkorn University, Grant CEB_D_9_2006, the TRF/BIOTEC Special Program for Biodiversity Research and Training, Grant T_249003, and the Commission on Higher Education, Thailand (the Cooperative Research Network - CRN).

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ABL	= scale on abaxial surface of lamina.
ADL	= scale on adaxial surface of lamina.
AW	= annulus width.
BALV	= large lateral vein at lamina base.
BK	= Department of Agriculture, Bangkok.
BKF	= National Park, Wildlife and Plant Conservation Department, Bangkok.
BM	= British Museum (National History Museum), London.
CA	= cluster analysis
DA	= discriminant analysis
E	= Royal Botanical Edinburgh, Edinburgh.
GSC	= Gower similarity coefficient
INDC	= occurrence of indurate cells.
K	= Royal Botanical Kew, London.
KUN	= Kunming Station of the Botanical Institute, Academia Sinica, Kunming.
L	= Rijksherbarium, Leiden.
LA	= lamina apex.
LASL	= length of the apical sterile portion of lamina.
LBS	= symmetry of lamina base.
LFPL	= length of the fertile portion of lamina.
LL	= lamina length.
LLLA	= ratio of lamina length and length of sori occurred area.
LLLT	= ratio of lamina length and lamina tip length.
LLST	= ratio of lamina length and stipe length.
LM	= lamina indentation.
LPL	= longitudinal posture of lamina margin.
LT	= lamina texture.
LV	= veins or lateral vein prominence on abaxial surface of lamina.
LW	= lamina width.
mm	= millimeter

NM	= number of meristele in rhizome.
NSSR	= number of sclerenchyma strand in rhizome.
P	= Laboratoire de Phanerogamie, Museum National d'Histoire Naturelle, Paris.
PE	= Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Academia Sinica, Beijing.
PHD	= phyllopodia diameter.
PHL	= phyllopodia length.
PYU	= Yunnan University Herbaium, Yunnan.
RHDM	= rhizome diameter.
RHLI	= longest rhizome internode length.
RHS	= rhizome surface.
RHSI	= shortest rhizome internode length.
RSAS	= apex of rhizome scale.
RSAT	= attachment of rhizome scale.
RSBS	= base of rhizome scale.
RSC	= clathrate appearance of rhizome scale.
RSCO	= colour of rhizome scale.
RSIP	= insertion point of rhizome scale.
RSL	= lobe of rhizome scale.
RSLE	= rhizome scale length.
RSM	= margin of rhizome scale.
RSOR	= orientation of rhizome scale.
RSS	= shape of rhizome scale.
RSUS	= appearance of hairs on upper surface of rhizome scale.
RSWI	= rhizome scale width.
S.L.	= sensu lato (in the broad sense).
S.S.	= sensu stricto (in the strict sense).
SL	= sorus length
SODBA	= sori distribution between lamina base and apex.
SOPO	= sorus position between midrib and margin.
SOR	= sori orientaion when compare with the closest midrib.
SORN	= sorus row number between midrib or rachis, and the margin.
SPL	= spore length.

SPOL	= sporangium length.
SPOW	= sporangium width.
SPW	= spore width.
STD	= stipe diameter at the middle of its length.
STL	= stipe length.
STOP	= stomium position.
STPH	= ratio of stipe length and phyllopodium length.
SW	= sorus width
TI	= Botanical Gardens, University of Tokyo, Tokyo.
μm	= micrometer

CHAPTER I

GENERAL INTRODUCTION

Pteridophytes are vascular plants. Their life cycle consisted of two separate free-living plants, i.e gametophytes and sporophytes. The gametophyte (haploid) tends to be inconspicuous and short live. Whilst the sporophyte (diploid) is more conspicuous and dominant plant and lives for an indefinite period (Boonkerd and Rossarin, 2000). Pteridophytes consisted of both extinct and living plants and Foster and Gifford (1974) classified the living pteridophytes into 4 classes i. e. Psilopsida, Lycopsida, Sphenopsida and Filicopsida. The latter class is known as the class of ferns. The morphological structures of fern sporophytes consisted of three main organs, i.e rhizomes, fronds and roots. Rhizomes usually are covered by scales. Fronds consisted of stipes and laminas and fronds form the crozier when young. Laminas are simple or compound (having the lamina divided into two or more distinct pinnae or pinules). The parts of the fern plant are shown in Figure 1.1.

The family Polypodiaceae is one of thirty-three families of the Filicopsida (Kubitzky, 1990). It consisted of about 50 genera and 600 species. The general features of the members of this family are as following: terrestrial or epiphytic, sometimes epilithic; rhizome covered by clathrate scales (i.e, the scales having cells structure having darkened partitions between adjacent cells only) (Figure 1.2 A). Fronds monomorphic to strongly dimorphic, mostly articulated to phyllopodia (i.e. an outgrowth from the stem to which a stipe is articulated) (Figure 1.2 B); lamina simple, lobed to pinnatifid or simply pinnate to bipinnate; Sori usually rounded exindusiate, sometimes protected when young by paraphyses (i.e. sterile structure occurring among the sporangia of some ferns) (Figure 1.2 C); sporangia short- to long stalk and capsule with vertical annulus (i.e. annulus consisted of indurate cells, epistomium, stomium and hypostomium) (Figure 1.2 D) (Hennipman et al., 1990).

The genus *Lepisorus* (J. Smith) belongs to the large fern family Polypodiaceae. In the broad sense, the genus *Lepisorus* Ching s.l. (including the *Paragramma*) comprised approximately 30 species (Verdcourt, 2001), 40 species (Hennipman et al., 1990) or 70 species (Lin, 2000), naturally occurring in the tropical and subtropical old world and extending northwards to the Far East of Russia with one species in Hawaii

(Verdcourt, 2001) (Figure 1.3 A). However, the *Paragramma* comprise 2 species (Copeland, 1947) distributed in New Guinea, Sumatra, Malay Peninsula, Thailand, Java Borneo, Philippines, Celebes, Himalayas, Vietnam (Hovenkamp 1998c). The members of *Lepisorus* s.l. are epiphytic, epilithic or terrestrial ferns with short to long-creeping rhizome covered with clathrate scales. Fronds are monomorphic, and laminas are simple, entire and mostly naked while the sori are in single rows on either side of the costa and covered with clathrate paraphyses (Hennipman et al., 1990; Verdcourt, 2001). In the strict sense, however, *Lepisorus* sens.str. (excluding the *Paragramma*) was firstly treated by J. Smith (1846) as a section of highly heterogeneous *Drynaria*. Ching (1933) later raised the section *Lepisorus* to generic rank. An example of general morphology and habit of *Lepisorus* sp. is shown in Figure 1.4.

Subsequently, the taxonomy of *Lepisorus* has been the subject of intensive research for more than 70 years from the date of its establishment. From the last five decades, researchers have aimed to work intensively for monographs or revisions of the other fern genera in Polypodiaceae, for example *Goniophlebium*, *Thylacopteris* and *Polypodiopteris* (Rödl-Linder,1990, 1994a, 1994b), *Platycerium* (Hennipman and Roos, 1982), Drynarioideae (Roos, 1985), *Pyrrosia*, *Paraselliguea* and *Selliguea* (Hovenkamp, 1986, 1997, 1998), *Microsorum* (Bosman, 1991) and Microsoriod ferns (*Microsorum*, *Leptochilus* and *Podosorus*) (Nooteboom, 1998), and *Platygyria* (Zhang et al., 2003). Although the need for revision is urgent and has been strongly recommended (Holttum, 1973), the revisions for the whole range distribution of *Lepisorus* s.l. have never been completed. Despite the urgency of the need for revision of the genus *Lepisorus*, this work cannot be fulfilled without a clarification of the generic circumscription. It is likely that this more important work should be performed prior to, or at the same time that the other parts of the revision are carried out.

To date *Lepisorus* is one of the most controversial fern genera regarding to its taxonomic status. Based on external morphology, small taxa, i.e. *Paragramma* and *Platygyria*, have sometimes been treated by some pteridologists to include or exclude in *Lepisorus*, and *Platygyria* have sometimes been treated by some pteridologists as a synonym of *Neocheiropteris*, while the others still kept the related taxa as three distinct genera.

The genus *Neocheiropteris* was established based on *N. palmatopedata* Christ as a type species. It distributed from north-eastern India east to Japan and south to

Malesia (Hennipman, 1990) (Figure 1.3 B). The genus is epiphytic or terrestrial fern and has tufts of hairs on rhizome scales. The general morphology and habit of *N. palmatopedata* Christ is shown in Figure 1.5. On the other hand, the fern genus *Platygyri*a was established based on a combination of *Platygyria waltonii* Ching by Ching and Wu (1980). The distribution of this genus is east and west Himalaya, the Sichuan and Yunnan Provinces of China and India (Yu and Lin, 1995; Ghosh et al., 2004) (Figure 1.3 C). Recently, five species were recognized as *Platygyria* spp. (Zhang et al., 2003). The general morphology and habit of *Platygyria waltonii* (Ching) Ching & S.K. Wu is shown in Figure 1.6.

Based on Hennipman et al. (1990), the family Polypodiaceae was divided into 2 subfamilies named Platycerioideae and Polypodioideae wherein the first subfamily was distinguished from the latter by leaves bearing stellate hairs. Based on the combination of characters of leaf, rhizome scales and spores, the latter subfamily was composed of 6 tribes i.e. Drynarieae, Lepisoreae, Loxogrammeae Microsoreae, Polypodieae and Selligeeae. The Lepisorae tribe, that was defined based on characters comprising clathrate rhizome-scales, absence of humus-collecting fronds, generally entire lamina, absence of stellate hairs on the fronds, thick exospore and inconspicuous perispore, comprise the largest genus, *Lepisorus* s.l., and small genera i.e. genus *Belvisia, Drymotaenium and Lemmaphyllum*. In the descriptions provided by Hennipman et al. (1990), genera in tribe Lepisoreae have sori covered by clathrate paraphyses. However, the genera in this tribe are distinct from the other genera as following: (1) the genus *Lepisorus* has monomorphic fronds and sori forming one row between midrib and margin, (2) the genus *Bevisia* has monomorphic fronds, coenosori (i.e. fused sori) on apically contracted segment, (3) genus *Drymotaenium* has monomorphic fronds, sori forming a line of coenosori between the midrib and lamina margin, and genus *Lemmaphyllum* mostly has dimorphic fronds and coenosori.

Details of infrafamilial classification of family Polypodiaceae proposed by Hennipmen et al (1990) was shown in Table 1.1

- Family Polypodiaceae
  - Subfamily Platycerioideae
  - Subfamily Polypodioideae
    - Tribe Drynarieae
    - Tribe Lepisoreae
      - Genus *Lepisorus* (J.Sm.) Ching sens.str. (including *Paragramma* T.Moore)
      - Genus *Belvisia* Mirbel
      - Genus *Drymotaenium* Makino
      - Genus *Lemmaphyllum* C. Presl
    - Tribe Microsoreae
      - Genus *Christiopteris* Copel.
      - Genus *Lecanopteris* Reinwardt
      - Genus *Colysis* C. Presl
      - Genus *Leptochilus* Kaulf.
      - Genus *Microsorum* Link
      - Genus *Neocheiropteris* Christ (including *Playgyria* Ching & S.K.Wu)
      - Genus *Dictymia* J.Sm.
      - Genus *Phymatosorus* Pic.Serm
    - Tribe Loxogrammeae

Table 1.1 Infrafamilial classification of Polypodiaceae (Hennipman et al., 1990)

In 1960s, the call for criteria of systematics to be applied to taxonomic decisions, for example criteria for determining whether or not a specimen belong to a new taxon, exploring relationships existing between the members of a group of taxa. Therefore, two important methods were developed in that time. One of these was known from its inception as numerical taxonomy that now a day frequently and perhaps more appropriate refered to as phenetics in the strict sense (Quicke, 1993). Then, numerical taxonomy was largely developed and popularized by Sneath and Sokal (1973). In addition, more or less the same time, the other different method, known as cladistics or evolutionary systematics were also developed starting from German entomologist, Willi Hennig who published a book on phylogenetic systematics in 1950.

Until now, no systematic studies have been conducted to clarify the delimitation of *Lepisorus,* which has been contradicted by previous pteridologists, especially in the case of studies based on the phenetic relationships to its related taxa. In the phylogenetic field, however, few attempts have been made to clarify the phylogenetic relationships within *Lepisorus*, or between *Lepisorus* and related genera. Moreover, these occasional attempts were not performed in an overly comprehensive sense.

The most recent preliminary and broadly phylogenetic analyses among *Lepisorus* sens.str. and related genera were performed by Schneider et al. (2004) who explored the phylogeny of polygrammoid ferns (family Grammitidaceae and Polypodiaceae). The result determined that relationships of the *Lepisorus* sens.str. and *Platygyria* remain dubious and the monophyletic *Lepisorus* and *Platygyria* remains questionable and requires further analysis.

Research Objectives

As previously mentioned, until now, no taxonomic studies have been aimed at clarifying the circumscriptions for these taxa.

The core objectives of this thesis, therefore, are the phenetic and phylogenetic analyses of the *Lepisorus*, *Paragramma* and *Platygyria*. Both analyses were conducted using morphological and anatomical characters. The UPGMA clustering and discriminant analyses were chosen for the phenetic analyses, and the maximum pasimony method was selected for the phylogenetic analysis,. In addition, anatomical surveys of rhizome and morphology were performed while preparing the data set for the analyses.

The objectives for the phenetic relationship study in the present work were to investigate the phenetic relationship and determine the suitability of the generic circumscriptions of *Lepisorus* and the related genera, i.e. *Paragramma*, *Platygyria* and *Neocheiropteris*.

The objectives for of the phylogenetic relationship study in the present work were as follows: (1) to evaluate the critical delimitation of the genus *Lepisorus* genus and the other two related genera, i.e. *Paragramma* and *Platygyria*, that were occasionally either included in or excluded from it, (2) to investigate the relationships of the *Lepisorus* sens.str., *Paragramma*, *Platygyria* and the genus *Neocheiropteris*.

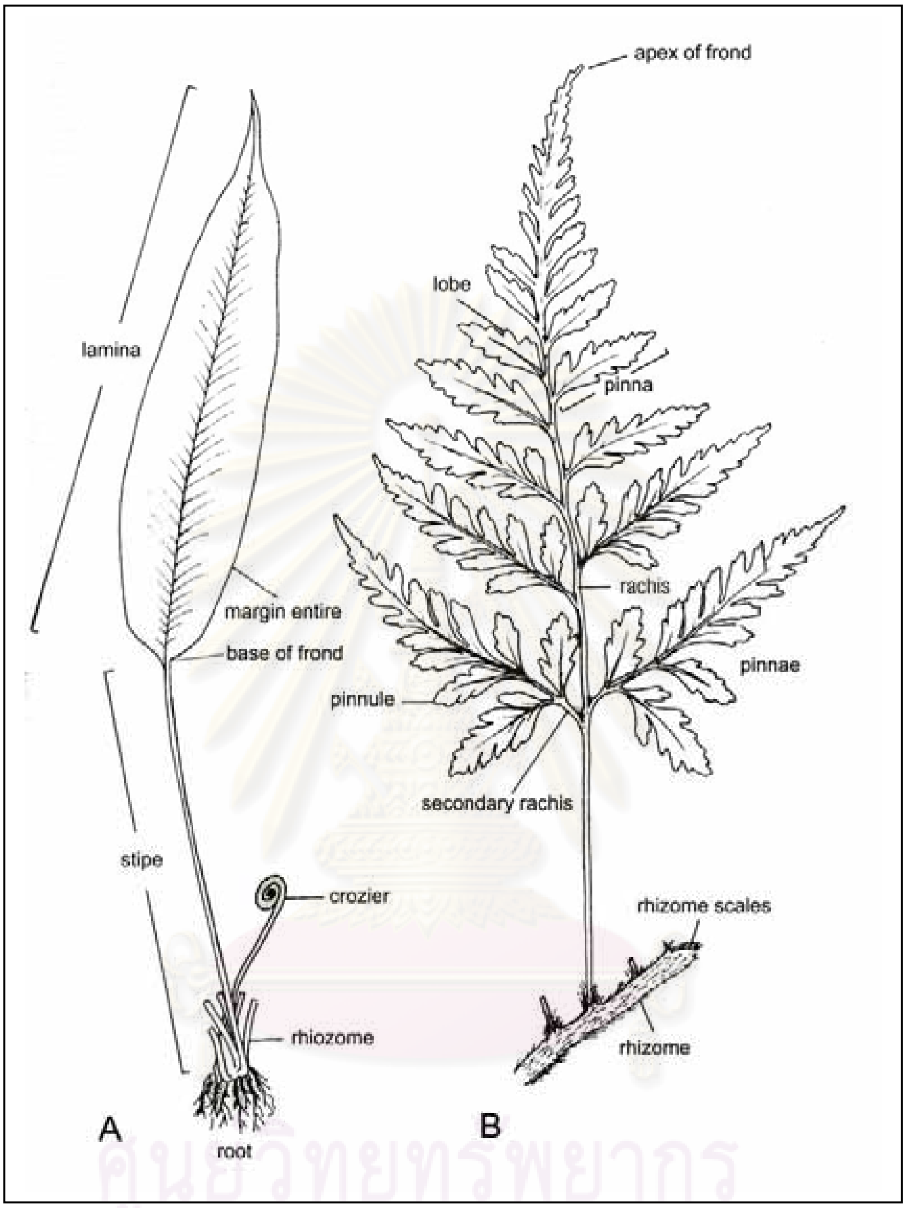

Figure 1.1 The parts of entire the ferns plant. A. fern having simple fronds, B. fern having bipinnate fronds (modified from Goudey, 1989).

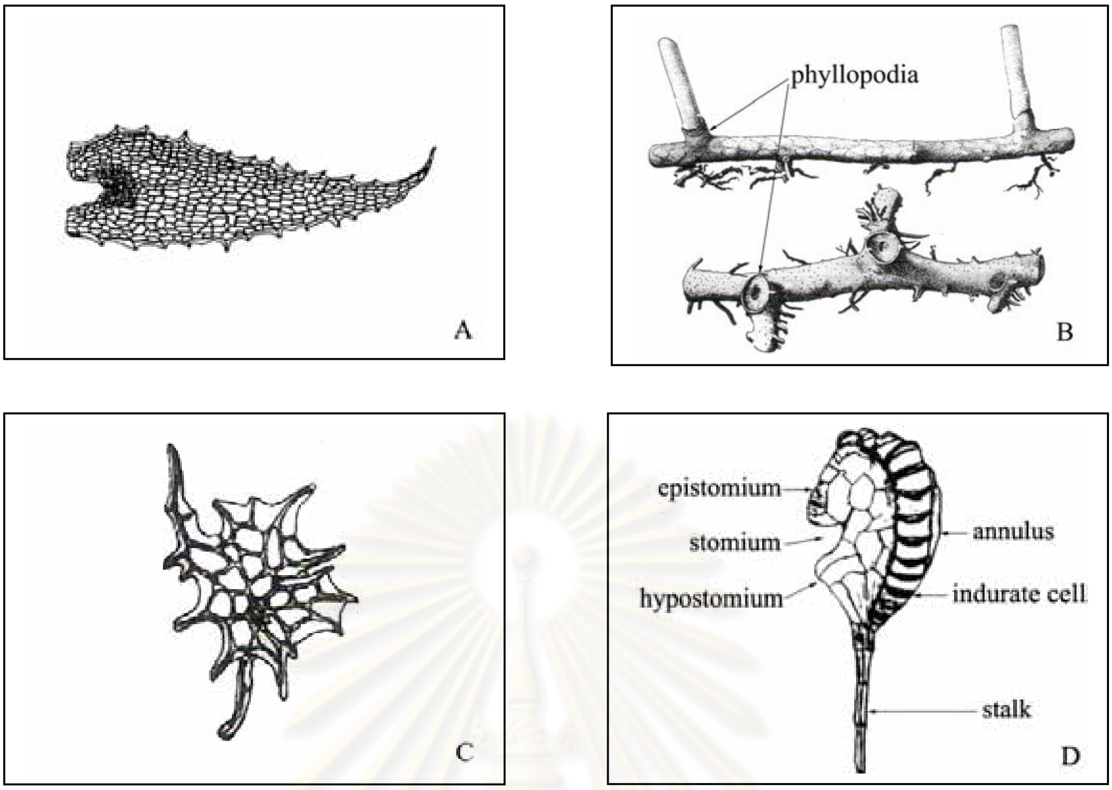

Figure 1.2 Some morphological characters of some species Polypodiaceae. A. Scale of *Polypodium microrhizome* Clark ex Bak. (Devol and Kua (1975), B. Phyllopodia of *Pyrrosia abbreviata* Tagawa (upper figure) and *P. platyphylla* Hovenkmp (lower figure) (modified from Hovenkamp 1976), C. Paraphysis of *Microsorum ensata* H.Ito Devol and Kua,1975) , D. Sporangium and its structures of *Polypodium microrhizome* Clark ex Bak. (modified from Devol and Kua (1975)

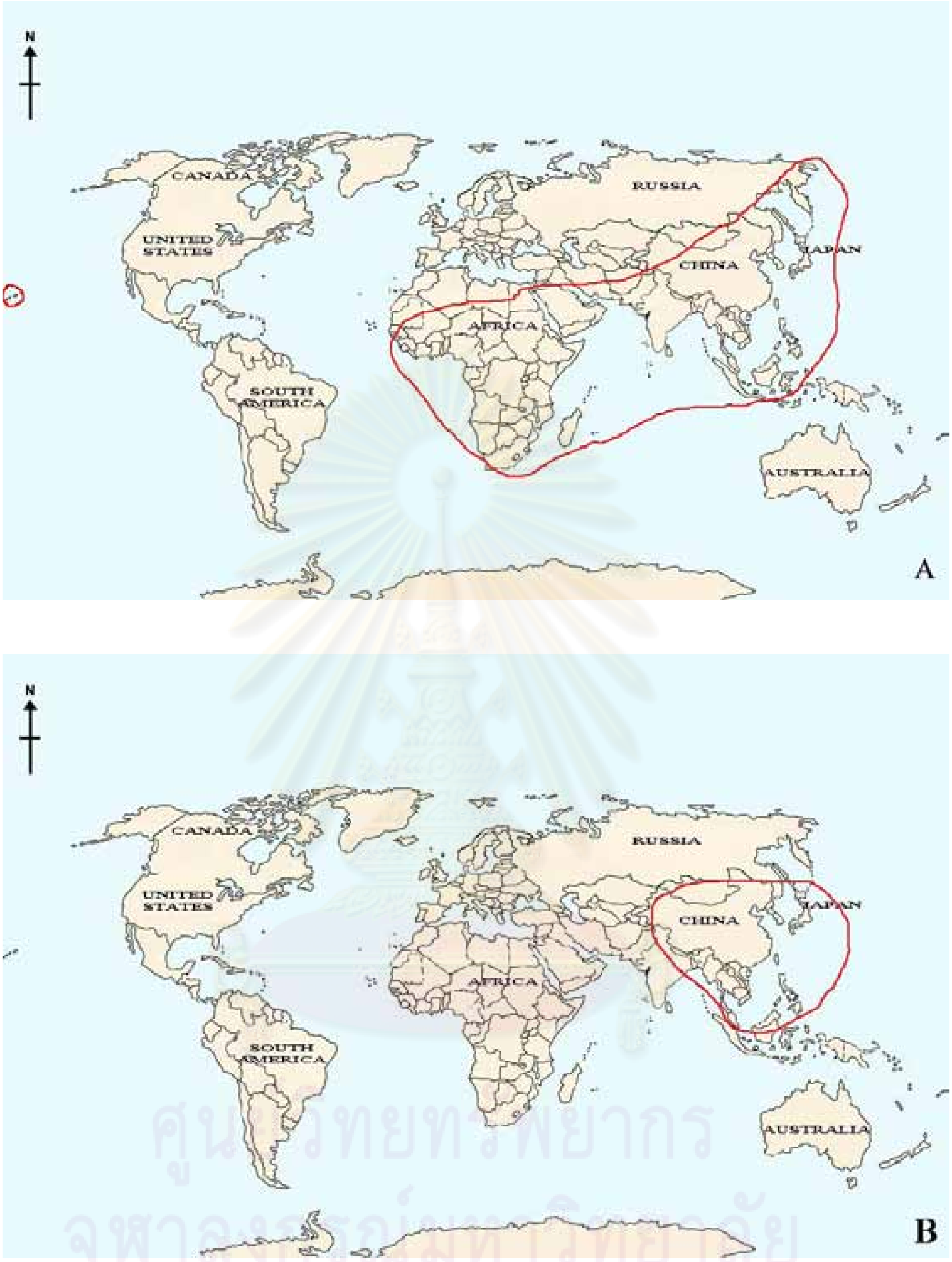

Figure 1.3 Distribution of studied taxa. A. *Lepisorus* s.l., B. *Neocheiropteris,* C. *Platygyria*.

Figure 1.3 (continued).

Figure 1.4 The general morphology and habit of the genus *Lepisorus nudus* (Hook.) Ching.

Figure 1.5 The general morphology and habit of the genus *Neocheiropteris palmatopedata* Christ.

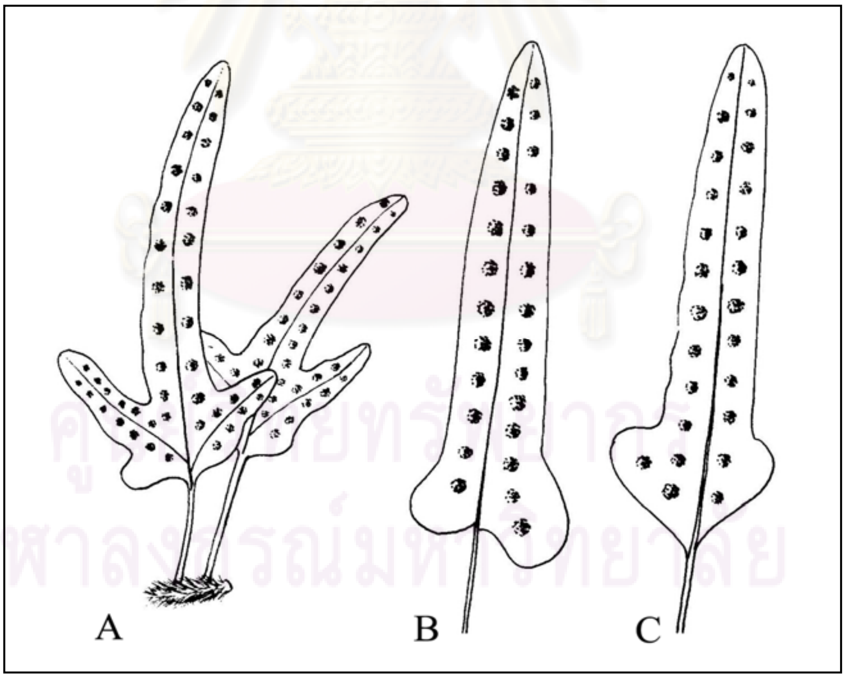

Figure 1.6 The general morphology and habit of the genus *Platygyria waltonii* Ching & S.K.Wu (ca.×1). A. entire plant, B. and C. laminas (Zhang et al., 2003)

CHAPTER II

LITERATURE REVIEW

2.1 Taxonomic History

Lepisorus was first established by J. Smith in 1846 as a section of highly hetergenous *Drynaria* apart from the sections *Phymatodes*, *Phyllitidis* and *Drynaria*. At the time, only *D. sesquipedalis* Wall., formerly a nomen nudum, which was validated at the same time through brief description, was included in this section. However, *Pleopeltis nuda* Hook., which is respected as a type species of section *Lepisorus* was cited as the synonym.

Thunberg (1784), a swedish taxonomist, made the first description for a taxon now included in *Lepisorus* when he described a Japanese *Polypodium lineare* Thunberg, which had to be called *Lepisorus thunbergianus* (Kaulf.) Ching. In 1801, Swartz added *Polypodium simplex* from the Réunion but the name was illegitimate because the earlier name, *Polypodium simplex* N. L. Burm (published in 1768), was recognized as a synonym for a species described independently as *Polypodium excavatus* by Willdenow in 1810. The *Polypodium elongatum* Schrader (now *L. schraderi* (Mett.) Ching) from continental Africa was described by Schrader in 1818, followed by *Pleopeltis nuda* Hook. from northern India by Hooker in 1823, *Pleopeltis elongate* Kaulf. from Hawaii by Kaulfuss in 1824 and *Polypodium scolopendrium* Ham. ex D.Don from Nepal by D. Don in 1825. Wallich (1828) listed *Polypodium loriforme* Wall., *Polypodium sesquipedale* Wall. from Nepal and *Polypodium gladiatum* Wall. from Nilgili Mountain in southern India, but these were considered nomen nodum. In addition, the botanists, namely, Kunze (1850 and 1851), Regel (1861 and 1881), Franchet and Savatier (1875), Clarke (1880) and Baker (1885), added new species collected mainly from China and Japan.

Christensen (1906) compiled the Index filicum and proposed concept and boundery of *Polypodium* as a large genus with included a number of subgenera and sections. Among these, he recognized the *Lepisorus* as a section of a subgenus, *Pleopeltis* Humb. & Bonpl. ex Willd., that was originally established for the New World Polypodiaceae.

The following ferns are now included in *Lepisorus*: four species and four varieties collected from the German colonies in West and East Africa were added by Hieronymus (1911); eight new taxa were described by Hayata (1909, 1914, 1915 and 1919) when he dealt with Taiwanese specimens; and fourteen Asian species and a number of infraspecific taxa (i.e. varieties and form) were recognized by Takeda (1915) who provided a special reference to the Chinese species.

Ching recognized 30 Chinese taxa and provided new combinations for the African taxa in 1933. He was the first taxonomist who recognized the differences between *Lepisorus* and *Pleopeltis*, In addition, Ching raised the section *Lepisorus* to generic rank while raising several other infraspecific ranks to specific ranks. Although the study of Ching (1933) was an important classical work for the taxonomy of the Chinese species, this work was recently revised by Lin (2000) who recognized 68 species. Furthermore, the 28 species collected from Yunnan Privince were also recognized by Cheng (2005).

In Asia, Iwatsuki (1991) recognized 9 species of *Lepisorus* when he wrote the book “Ferns and fern allies of Japan”. Shieh et al. (1994) recognized 11 species of *Lepisorus* in the Flora of Taiwan.

Bir and Satija (1981) revised *L. kashyapii* (Mehra) Mehra in India, stating that 3 varieties of this species were recognized. Bir and Trikha (1969) revised *Polypodium lineare* complex and allied species wherein 13 species of *Lepisorus* were recognized. In addition, Bir and Trikha (1974) revised the *L. excavatus* group wherein 9 species and 5 varieties were recognized.

Tardieu-Blot and Christensen (1939-51) studied Indochinese ferns wherein 10 species were recognized as belonging to the genus *Lepisorus*. The Malayan species was revised by Holttum (1955) and a more recent revision was performed by Hovenkamp (1998a, c) who revised the genus for the whole Malesiana region. The first author recognized only *L. longifolius* (Blume) Holtt, formerly treated as a *Paragramma* species, as belonging to *Lepisorus* while the second author added 3 other *Lepisorus* species including *Lepisorus balteiformis* (Brause) Hovenkamp that previously was *Paragramma. balteiformis* Brause.

In Thailand, 11 species (including a *P. longifolius* (Bl.) T. Moore) were recognized by Tagawa and Iwatsuki (1989) when the Flora of Thailand was published.

The taxonomic revisions for all African *Lepisorus* species were performed by Zink (1993), who recognized 9 species i.e. *L. bampsii* (Pichi Serm.) M.J. Zink, *L.*

excavatus (Willd.) Ching, *L. mildbraedii* (Hieron.) Pichi Serm., *L. perrierianus* (C.Chr.) Ching, *L. phlebodes* (Kunze ex Mett.) Ching, *L. preusii* (Hieron.) Pichi Serm., *L. rotundus* (Bonap.) Ching, *L. schraderi* (Mett.) Ching and *L. vesiculari-paleaceus* (Hieron.) Pichi Serm. Furthermore, the East African species were studied by Verdcourt (2001) who recognized 2 species whereas the five species formerly recognized by Zink (1993) were reduced to be synonyms of *L. excavatus* (Willd.) Ching.

The genus *Paragramma* was founded by T. Moore in 1857 and designed *P. longifolia* T. Moore as a type species (Copeland, 1947). To date, however, its separation from *Lepisorus* sens.str. has never been clear (Hovenkamp, 1998a). The recognition to maintain this genus as distinct genus was followed by Ching (1940), Copeland (1947) and Pichi Sermolli (1977). Copeland (1947) used the combined characters of shape of sori and the presence of lamina scales to distinguish *Paragramma* from his *Pleopeltis* s.l. (i.e. including *Lepisorus* sens.str. and excluding *Paragramma*). Two species, *Paragramma balteiformis* Copeland and *Paragramma longifolia* T. Moore were recognized by Copeland (1947). In contrast, Holttum (1955), Tagawa and Iwatsuki (1989), Hennipman et al. (1990) and Hovenkamp (1998a, c) agreed to unite *Paragramma* with *Lepisorus* sens.str.

The Chinese fern genus *Platygyri*a was established based on *Platygyri*a *waltonii* Ching as a type species (i.e. previously, *Platygyri*a *waltonii* Ching was *Neocheiropteris waltonii* Ching) and using the characters of sporangium as important defining characters. In addition, two other species, namely, *P. sinuata* Ching & S.K. Wu and *P. inaequibasis* Ching & S.K. Wu belonged to this genus (Ching and Wu, 1980). Three years later, *P. variabilis* Ching & S.K. Wu, *P. kongtingensis* Ching & Y.X. Lin and *P. muliensis* Ching & S.K. Wu were added to *Platygyria* (Ching et al., 1983). Zhang et al. (2003) then agreed to keep *Platygyria* at the genus level and accepted 5 species including a new combination of *Polypodium soulieanum* Christ as member of *Platygyria* and treating *P. kongtingensis* Ching & Y.X. Lin, and *P. muliensis* Ching & S.K. Wu as the synonym of *P. variabilis* Ching & S.K. Wu. There were, however, two other treatments of taxonomic position for *Platygyria*. The first involved putting *Platygyria* p.p. under *Neocheiropteris* s.l. (Ching, 1933; Hennipman et al., 1990). while the second involved accepting a combination of *Platygyria* p.p. and *Lepisorus* sens.str. (Yu and Lin, 1997; Fraser-Jenkins, personal communication, 2008). The *Neocheiropteris* was founded in 1905 by H. Christ, and it has pedatifid lamina and tufts of hairs on rhizome scales. Consequently, the combination of *Platygyria* with either *Lepisorus* sens.str. or s.l., or *Neocheiropteris* sens.str. or s.l., or its acceptance as a distinct genus requires further assessment.

Hennipman and Roos (1983) used spore ultrastructure from transmission electron microscope (TEM) for delimiting infrafamiliar groups within Polypodiaceae. Based on a *Lepisorus* type of spore later renamed *Belvisia* with a thick exospore (2-4 µm) throughout transversed by narrow cannals and showing a characteristic tangential banding, but lacking a so-called microcannal, they defined a group of these genera. Hennipman et al. (1990) used the details of Hennipman and Roos (1983), the characters of leaf indument and rhizome scales to provide the infrafamilial classification of Polypodiaceae. Details of infrafamilial classification of family Polypodiaceae proposed by Hennipmen et al (1990) was shown in Chapter I.

2.2 Methodological Review

2.2.1 Review of Morphological and Anatomical in *Lepisorus*

A few taxa have been investigated by Indian botanists as follows: *L. thunbergianus* and *L. excavatus* were studied by Khare (1965); and *L. kashyapii* (Mehra) Mehra, *L. macrosphearus* (Bak.) Ching and *L. subrostratum* (Hook.) C. Chr. were studied by Shivastava (1967). Shivastava reported that the three species studied had features as following: creeping and dictyostelic rhizome, rhizome and sori covered by clathrate scales, annulus having many indurate cells, numerous sclerenchyma strands scattered in ground tissue of rhizome.

Ogura (1972) proposed an important book on morphological and anatomical vegetative organs of pteridophytes. The descriptions of the characters detailed in that book were taken from his previous works and papers published by other researchers. With regard to the Polypodiaceae, he showed the details of morphological or anatomical characters of rhizomes, rhizome scales, fronds and roots. However, there was no report of morphology and anatomy of genus *Lepisorus*, *Paragramma*, *Platygyria* and *Neocheiropteris*.

Zink (1993) studied morphology and anatomy of African *Lepisorus* species. The organs that he studied were rhizome, indument, leaf, and sorus. In addition, he showd some important characters can be used to distinguish genus *Lepisorus* and genus *Pleopeltis,* for example sclerenchyma strands and scales clathrate throughout were found in genus *Lepisorus* while sclerenchyma strands absent and centrally clathrate scales were found in genus *Pleopeltis*.

Yu and Lin (1997a) reported an examination of the rhizome and stipe anatomy of many *Lepisorus* species. In their report, they gave details of a number of vascular bundles in the rhizomes and stipes. Then, Rahaman and Sen (1999) reported the distinction of the fern genera *Lepisorus* and *Pleopeltis* Humb. et Bonpl. ex Willd. based on morphological and anatomical characters such as the presence of numerous sclerenchyma strands in the rhizomes and the absence of lobes on the base of the rhizome scales of *Pleopeltis* while the absence of the same strands and presence of the same lobes were found in *Lepisorus*.

2.2.2 Review of Phenetic Relationship in ferns

In ferns, the examples of using phenetics in systematics are as follow: Pollawat (1996) investigated the variation within and among 7 populations of *Pyrrosia eberhardii* (Christ.) Ching, she concluded that there were some variations within and between populations, but these variations were still inadequate to distinguish any population as infraspecific taxon or a new separated species. Thomson (2000) used 27 morphological characters in multivariate analyses to assess the validity and taxonomic status of subspecies and varieties of *Pteridium* (Dennstaedtiaceae). It was showed that var. *africanum*, var. *arachnoideum*, var. *esculentum*, var. *latiusculum* and var. *revolutum* can be separate from each other. McHaffie, Legg and Sydes (2002) used 14 morphological characters in multivariate analysis to reveal morphological distinction between *Athyrium distentifolium* var. *distentifolium* Tausch ex Opiz. and var. *flexile* (Newman) Jermy. The result showed that the two varieties are clearly separated with only a few intermediates. Boonkerd (2003) examined morphological variation within populations and among population of three populations of *Doryopteris ludens* J.Smith. occurring in Thailand. Using cluster and discriminant analyses, two morphological varieties of these fern was found.

2.2.3 Review of Relationship in Ferns

So far many phylogenetic relationships of ferns has been explored phylogenetic analyzes and these analyzes were based on molecular and morphological data. The following are examples of study of phylogeny in ferns.

Van Uffellen (1993) proposed that genera *Belvisia*, *Drymotaenium*, *Lemmaphyllum* and *Paragramma* are ralared to genus *Lepisorus*.

Pryer et al. (1995) were the first team who used parsimony methods to analyze morphological data in ferns. Results based on 77 parsimony-informative characters showed that the genus *Polypodium* (the only representative taxon chosen for the family Polypodiaceae) was placed on a clade with the genus *Davallia*. However, a bootstrap support of this clade was lower than 50% (a 50% majority rule consensus of 3,326 the most parsimonious trees). Schneider (1996) used cladistic analysis to infer relationships among major groups of ferns based on 146 morphological characters, including 22 root characters. The *rbcL* tree determine that the genus *Polypodium* (Polypodiaceae) is sister to genus *Micropolypodium* (Grammitidaceae).

Dubuisson (1997) tested the classification of genus *Trichomanes* s.l. (Hymenophyllaceae) using 31 morphological and anatological characters, in general the result confirmed Morton‘s classification (1968). Hauk, Parks and Chase (2003) examined the infrafamilial relationships of Ophioglossaceae using 20 morphological characters. The result showed that there are two main clades, i.e. ophioglossoid and botrychioid clades, and revealed the relationships among genera of this family. Hennequin (2003) explored the phylogeny within the fern genus *Hymenophyllum* s.l. using morphological and cytological characters. It was found that the most probable basal elements of the *Hymenophyllum* are *Cardiomanes*, *Hymenoglosum*, *Diplophyllum and Mucodium*.

In addition, while monographs of the genera in the family Polypodiaceae, e.g. *Platycerium* (Hennipman and Roos, 1982), *Drynaria* and *Aglaomorpha* (Roos, 1995), *Pyrrosia* (Hovenkamp, 1986) and *Microsorum* (Bosman, 1991), were carried out, the phylogenetic relationships between the species of them were explored based on morphological or anatomical data and can be used to explore the relationships within these genera.

Recently, a preliminary of phylogenetic analyses among the *Lepisorus* sens.str. and related genera was performed by Schneider et al. (2004) to explore the global phylogeny of polygrammoid ferns (families Polypodiaceae and Grammitidaceae including 3 *Lepisorus* species, 1 *Platygyria* species and a few species of other related genera) utilizing the three chloroplast genome regions e.g *rbcL*, *rps4* and *rps4-trnS* intergenic spacers. The results indicated that *Lepisorus* sens.str. is paraphyletic. Nevertheless, the tree topology of this clade was not fully resolved.

CHAPTER III

MORPHOLOGICAL AND ANATOMICAL STUDY

3.1 Introduction

The morphology of an organism has been and remains the type of data used for most plant classification. Morphological features have the advantage of being easily observed; hence, their variability has been much more appreciated than other kinds of features. To outline the history of the use of morphology in plant taxonomy is to describe the development of the entire field. From the earliest recorded observations of the ancient Greeks (i.e., Theophrastus, 370-285 B.C.), through the age of the herbalists (1470-1670), into the early classifiers such as Ray (1686-1704), Linnaeus (1753), de Jussieu (1789), de Candolles (1844-1873), Bentham and Hooker (1862-1883) and so on to the systems of today e.g. Dahlgren and Clifford (1986), Dahlgren, Clifford and Yeo (1985) and so on, morphology has been dominant as researchers have based studies largely upon morphological data. That is to say that we have used, are still using, and will likely continue to use morphology (Stuessy, 1990).

Anatomy represents another classical source of data used in plant taxonomy and anatomical data are often extremely useful in solving problems of relationships. Furthermore, the use of anatomical data in systematics is long and follows in parallel fashion the use of more explicit morphological data (Stuessy, 1990). The anatomical studies of plant organs on both living and fossil pteridophytes were increasingly undertaken in the latter half of the 19th century (Ogura, 1972).

3.1.1 Chapter aims

According to the details in Chapter II, there are no comparative morphological and anatomical studies in the *Lepisorus* and related taxa, i.e. *Paragramma* and *Platygyria*, and genus *Neocheiropteris*. Therefore, morphological and anatomical examinations of them are performed in this research.

3.2 Materials and Methods

The morphological and anatomical characters involved in the present study, approximately 2,500 herbarium specimens from around the world and remaining in the herbaria of Europe (BM, E, L, K and P) and Asia (BKF, BK, KUN and PYU), as well as personal collections collected from China and Thailand, were studied. The total number of complete specimens selected for the examination comprised 520 specimens (Appendix 2). The specimens included in this study belonged to *Lepisorus* sens.str. (36 species) and its related genera i.e. *Paragramma* (2 species) and *Platygyria* (4 species) with specimens from the type species of each genus. Most of these specimens were identified by examining type specimens, whereas others were specimens determined by Bir and Trikha (1969) or M. J. Zink (i.e. determined on herbarium sheets) or Ching (1933) or Zhang et al. (2003). Other identifications were made by consulting literature i.e. Ching (1933), Hovenkamp (1998a, c), Zink (1993), Shieh et al. (1994), Verdcourt (2001), Tagawa and Iwatsuki (1989) and Zhang et al. (2003).

Because *Platygyria* species were sometimes merged with the genus *Neocheiropteris* by some previous pteridologists, *N. pamatopedata* H. Christ (i.e. the type species) specimens were also included in order to compare their morphology and anatomy.

The examination in this study was based on mature sporophytes and concerned rhizomes, rhirome scales, fronds, sori, sporangiums and spores.

3.2.1 Preparation for rhizome-anatomy study

The method of Nooteboom (1997) was followed with some additional details in preparation for the cross section of both dry and fleshy rhizomes by cutting with a sharp knife. The rhizomes that were chosen for study were at about 6-10 cm below the apex to ensure maturity, and examinations were conducted under a stereomicroscope (Zeiss stereo (Stemi DV4) or hand lens.

3.2.2 Scale preparation

A modified method of scale preparation adapted from the study of Hovenkamp (1986) was also followed wherein the rhizome scales were wetted with a strong solution of photographic detergent (KODAK photo-pho 200: water–appr. 1:3), left for a few minutes and then carefully lifted from the rhizome. The scales were then rinsed in water, kept in glycerin-jelly and place on permanent slides. Scale-morphology study was carried out by using a Keiba digital caliper No. 111-101HB or they were studied under the Zeiss stereo (Stemi DV4) or Olympus light (CH30) microscopes.

3.2.3 Morphological study for the other organs

The morphological study for the other organs was conducted by observation. Small organs were examined under Zeiss stereo (Stemi DV4) or Olympus light (CH30) microscopes and measurements were carried out using a Keiba digital caliper No. 111-101HB, or a micrometer.

3.3. Results and Discussion

3.3.1 *Lepisorus* (J.Sm.) Ching sens.str.

Rhizome short- to long-creeping, rarely branched, up to 46.77 mm internode long, 0.6-7.8 mm in diameter, dorsiventrally slightly flattened to almost terete, glaucous or not, the one without glaucous has light brown to dark brown when dry, covered by clathrate scales; rhizome anatomy dictyostelic with the number of vascular strands ranges from 2 to 20 that formed a regular or irregular shape of ring, without sclerenchyma strands or up to about 128 strands pass longitudinally through the rhizomes of all species, light brown to dark brown when dry (Figure 3.1A). *Phyllopodia* (i.e. base of stipe which has specially enlarged structure) inconspicuous to distinct, 0.06-3.53 mm long, 0.15-3.58 mm in diameter, light to dark brown when dry.

Rhizome scales peltae or pseudopeltate or basifixed, clathrate with or without central opaque region, appressed or slightly spreading or strongly spreading, 0.6-8.5 mm long, 0.4-8.5 mm wide; shapes are mostly broadly ovate to triangular or leceolate, either evenly narrowed toward the apex from a slightly broader base; apex rarely obtuse or usually short to long broadly or narrowly acute or acuminate, frequently forming long and filiform tip that then breaking off easily; bases round or obtuse or cordate, sometimes forming 2-3 lobes; colour ferrugineous to castaneous or dark brown to black, concolourous or discolourous with darker central area (or central opaque region) and paler margin area; margins entire or erose to distinctly denticulate or dentate with few to numerous short to long spine-like teeth; hairs on upper surface are present or absent; insertion point at base or close to base more than apex or at the middle (Figure 3.2A,B,C).

Fronds remote or close, up to 46.77 mm apart, articulate to the rhizome, monomorphic; stipe slightly terete, 0.5-148.73 mm long, 0.12-13.76 mm in diameter, usually stramineous, occasionally yellow-brown to black orage or grayish-brown, glabrous or set with few scales similar to those of the rhizome; lamina simple, linear or narrowly elliptic to broadly elliptic or narrowly lanceolate to broadly ovate, 12.51-529.31 mm long, 52.55-16.35 wide, stramineous to deeply brown when dry; length of the apical sterile portion of lamina very short or up to 129.74 mm long; lamina apex acute or acuminate or obtuse or round; lamina base symmetric or nearly symmetric or asymmetric attenuate or cuneate; lamina margin entire or with a slightly sinuate margin, flat or slightly to strongly revolute; lamina texture membranaceous, chartaceous, subcoriaceous or coriaceous; lamina indument mostly absent on both adaxial and abaxial surfaces, or sparsely present (usually caducous); lamina scales consisting of various shape, light brown to black, clathrate, covering the costa or lamina and often restricted to the lower 1/2 or 1/3 of lamina; venation usually obvious or obscure, the obscure ones occurring on subcoriaceous and coriaceous lamina; venation reticulate, large lateral vein at lamina base absent.

Sori orbicular or elliptical or oblong or linear, 0.45-9.94 mm long, 0.25-12.2 mm wide, on either side of the costa, covered with paraphyses at least when young, superficial or slightly to deeply impressed and prominent on abaxial surface of the lamina, distributed on upper half or on upper half reaching to the lower half or only on lower half of lamina, medial between costa and margin to very close to the costa or to very close to margin; sori orientaion when compare with the closest midrib oblique or not; sporangium orbicular or elliptical or ovate, 150-525 µm long, 125-400 µm wide, light to dark brown; indurate cells many; annulus 35-87.5 µm wide (Figure 3.3A); stomium at the position between epi and hypostomium; spore elliptical or globose or subpyriform, 45.2-75 µm long, 25-62.5 µm wide, yellowish to yellow or light brown to brown; soral scales usually caducous at maturity, peltate, clathrate, umbrella-shaped or rather regular in outline, light-brown to black, subentire, shallowly to coarsely dentate (Figure 3.3C).

3.3.2 *Paragramma* T.Moore

Rhizome short- to slightly short-creeping or ascending, rarely branched, 0.48-20.04 mm internode long, 1.93-5.36 mm in diameter, dorsiventrally slightly flattened to almost terete, glaucous or not glaucous, not the glaucous ones light brown to dark brown when dry, covered by clathrate scales; rhizome anatomy dictyostelic with 3-28 vacular bundles, rarely without sclerenchyma strands or up to about 141 strands scattering in rhizomes, light brown to dark brown when dry (Figure 3.1B.); phyllopodia raised and distinct, 1.05-37.41 mm long, 1.74-4.75 mm in diameter, rarely light to usually dark brown when dry.

Rhizome scales peltate or pseudopeltate or basifixed, clathrate without central opaque region, appressed or slightly spreading or strongly spreading, 0.6-5.8 mm long, 0.35-1.8 mm wide; shapes are triangular or lanceolate or triangular, either evenly narrowed toward the apex from a slightly broader base; apex long (rarely short) and narrowly (rarely broadly) acute or acuminate, frequently forming long and filiform tip that then breaking off easily; bases round or obtuse or cordate; colour ferrugineous to castaneous or dark brown to black, one colour; margins distinctly denticulate or dentate with many short to long spine-like teeth; hairs on upper surface absent; insertion point at base or close to base more than apex. (Figure 3.2 D).

Fronds close or slightly close to each other, 0.48-20.04 mm apart, articulate to the rhizome, monomorphic. *Stipe* slightly terete, 3.16-95.48 mm long, 1.14-4.16 mm in diameter, usually stramineous or yellow-brown or brown, glabrous or set with some clathrate scales similar to those of the rhizome.

Lamina simple, long linear to narrowly lanceolate or narrowly ovate, 24.36-944.21 mm long, 8.63-45.21 mm wide, stramineous to deeply brown when dry; length of the apical sterile portion of lamina 1.88-39.12 mm long; lamina apex acute or acuminate or obtuse or round; lamina base symmetric or nearly symmetric or asymmetric attenuate or cuneate or obtuse; lamina margin entire or with a slightly sinuate margin, slightly revolute; lamina texture subcoriaceous or coriaceous; lamina indument few to low density of scales near the base near or on midrib, present on abaxial side (usually caducous), usually absent on adaxial side, the scales consisting of variously shaped, light brown to black, clathrate scales on the costa and/or the lamina often restricted to the lower haft of lamina; lamina veins or lateral vein obvious or obscure, the obscure ones occurring on coriaceous lamina; veinlets netted, large lateral vein at lamina base absent.

Sori orbicular or elliptical or oblong, 0.6-13.47 mm long, 0.6-3.72 mm wide, on either side of the costa, covered with paraphyses at least when young, superficial or slightly to deeply impressed and prominent on abaxial surface of the lamina, distributed on upper half or on upper half reaching to the lower half, medial between costa and margin; sori orientaion when compare with the closest midrib oblique; sporangium orbicular or elliptical or ovate, 225-375 µm long, 200-275 wide, light to dark brown; indurate cells many; annulus 45-68 µm wide; stomium at the position between epi and hypostomium; spore elliptical or slightly globose, 50-75 µm long, 38-55 µm wide, yellowish to yellow; soral scales usually caducous at maturity, peltate, clathrate, lanceolate to broadly ovate, umbrella-shaped, light-brown to black, shallowly to coarsely dentate.

3.3.3 *Platygyria* Ching & S.K.Wu

Rhizome short creeping, rarely branched, about 0.28 mm to 12.1 mm internode long, 1.03-2.47 mm in diameter, almost terete or rarely dorsiventrally slightly flattened, glaucous or not glaucous, the glaucous ones light brown to dark brown when dry, covered by scales; rhizome anatomy dictyostelic with 1-11 vascular bundles or without vascular bundle, without sclerenchyma strands or up to about 44 strands, light brown when dry (Figure. 3.1C.); phyllopodia inconspicuous, 0.38-2.34 mm long, 0.63-1.93 mm in diameter, light to slightly dark brown when dry.

Rhizome scales almost peltate or pseudopeltate (rarely basifixed), clathrate without central opaque region, appressed or slightly spreading or strongly spreading, 1.98-4.15 mm long, 0.8-1.8; shapes mostly broadly ovate to lanceolate, either evenly narrowed toward the apex from a slightly broader base; apex usually long (rarely short) narrowly (rarely broadly) acute or acuminate, frequently forming long and filiform tip that then breaking off easily; bases round or obtuse or cordate, without lobes; colour ferrugineous to castaneous or dark brown, almost concolourous; margins distinctly denticulate or dentate with many shorth to long spine-like teeth; hairs on upper surface present or absent; insertion point at base or close to base more than apex. (Figure. 3.2E.).

Fronds close to each other, about 0.28-12.1 mm apart, articulate to the rhizome, monomorphic. *Stipe* slightly terete, 6.5-93.5 mm long, 0.47-2.67 mm in diameter, usually stramineous, occasionally yellow-brown to black-brown, glabrous or set with few scales similar to those of the rhizome; lamina simple, slightly linear or narrowly lanceolate to oblong or broadly ovate, 29.05-218.96 mm long, 4.18-90.82 wide, stramineous to deeply brown when dry; length of the apical sterile portion of lamina 2.42-41.3 mm long; lamina apex acuminate or obtuse or round; lamina base symmetric or nearly symmetric or asymmetric attenuate or cuneate; lamina margin entire,slightly sinuate, auriculate, hastate or pedatifid, flat; lamina texture membranaceous chartaceous; lamina induments absent on both sides or sparsely present (usually caducous) on abaxial side, the scales consisting of variously shaped, light brown to black, clathrate scales on the costa and/or the lamina often restricted to the lower half of lamina; lamina veins or lateral vein usually obvious or obscure; veinlets anastomosing, large lateral vein at lamina base absent.

Sori orbicular or elliptical or ovate, 0.96-7.96 mm long, 0.87-3.83 mm wide, positioned on either side of the costa, covered with paraphyses at least when young, superficial on abaxial surface of the lamina, distributed on upper half or on upper half reaching to the lower half or only on lower half of lamina, medial between costa and margin or close to the costa; sori orientaion when compare with the closest midrib oblique or not oblique; sporangium mostly globose, 275-475 µm long, 245-325 µm wide, light to dark brown, indurate cells absent or few; stomium position not constant on annulus; annulus 120-230 µm wide (Figure 3.3B); spore elliptical or globose or subpyriform, 52.5-70 µm long, 33-65 µm wide, yellowish to yellow or light brown to brown; soral scales usually caducous at maturity, peltate, clathrate, slightly orbicular or broadly ovate to lanceolate, umbrella-shaped light-brown to black, subentire, shallowly to coarsely dentate (Figure 3.3 D.

3.3.4 *Neocheiropteris* Christ

Rhizome short- to long-creeping, rarely branched, internode 3.05-24.56 mm long, 2.55-7.06 mm in diameter, dorsiventrally slightly flattened to terete, not glaucous, light brown to dark brown when dry, covered by clathrate scales; rhizome anatomy dictyostelic with the number of vascular strands ranges from 5 to 15 that formed a regular or irregular shape of ring in rhizome, mostly without sclerenchyma strands or with sclerenchyma strands up to about 85 pass longitudinally through the rhizomes, light brown to brown when dry (Figure. 3.1D); phyllopodia inconspicuous, 0.61-2.94 mm long, 1.85-7.27 mm in diameter, brown when dry.

Rhizome scales basifixed or pseudopeltate, clathrate without central opaque region, appressed, 1.2-6.6 mm long, 0.9-3.25 mm wide; shapes lanceolate or triangular or ovate (rarely circular), either evenly narrowed toward the apex from a slightly broader base (except for the circular ones); apex usually short to long narrowly acute or acuminate, frequently forming long and filiform tip that then breaking off easily; bases round or obtuse, without lobe; colours ferrugineous or brown, discolourous or concolourous, without darker central area or central opaque band; margins distinctly denticulate or dentate with many short to long spine-like teeth; hairs on upper surface present on central region at least when young; insertion point at base or close to base more than apex. (Figure. 3.2F.)

Fronds remote or close, about 3.05-24.56 mm apart, articulate to the rhizome, monomorphic; stipe slightly terete, 72.68-625.89 mm long, 1.4-4.43 mm in diameter, usually stramineous or occasionally brown, glabrous or set with few scales similar to those of the rhizome; lamina simple, broadly ovate to circular in outline, 20.98-446.73 mm long, 41.23-376.75 mm wide, stramineous to deeply brown when dry; length of the apical sterile portion of lamina about 18.28-296.77 mm long; lamina apex obtuse or round; lamina base symmetric or nearly symmetric cuneate; lamina margin entire or pedatifid, flat; lamina texture membranaceous or chartaceous; lamina induments absent; lamina veins or lateral vein obvious; venation reticulate; large lateral vein at lamina base present or absent.

Sori more than 1 row between midrib and margin, orbicular or elliptical or oblong or ovate, 1.28-43.18 mm long, 0.71-3.9 mm wide, on either side of the costa, covered with paraphyses at least when young, superficial on abaxial surface of the lamina, distributed on lower half of lamina, close to midrib to close to the margin; sori orientaion when compare with the closest midrib oblique or not oblique; sporangium orbicular or ovate, 276.923-350 µm long, 200-240 µm wide, light to dark brown, indurate cells distinct, annulus 36-75 µm wide; stomium at the position between epi and hypostomium; spore elliptical or globose or subpyriform, 38.462-60 µm long, 23-40 µm wide, yellowish to yellow or light brown to brown; soral scales usually caducous at maturity, peltate, clathrate, umbrella-shaped, light-brown to black, subentire, shallowly to coarsely dentate.

Generally, rhizomes of these genera are short- to long creeping, raely branched. The rhizome surface is covered by clathrate scales, glaucous or not glaucous, bearing roots on ventral side and phyllopodia on dorsal side. Rhizome is dictyostelic. The vascular bundles form a ring in ground tissue, but it is absent in some specimens of the genus *Platygyria*, especially the small plants. Sclerenchyma strands in rhizome are absent or numerous and variously scattered (Figure 3.1). The genus *Platygyria* species usually lack or have a few sclerenchyma strands while the other genus *Neocheiropteris* usually have many sclerenchyma strands; however, *Neocheiropteris palmatopedata* Christ, the type species, lacks this strand. On the other hand, the genus *Lepisorus* and *Paragramma* usually have many or numerous sclerenchyma strands. As far as the rhizome anatomical characters were concerned, the difference between these ferns was not so distinct. However, most *Platygyria* species and *N. palmatopedata* Christ tended to have either fewer or total lack of vascular bundles and sclerenchyma strands in the rhizome (Figure 3.1C,D). Phyllopodia are conspicuous or inconspicuous. All rhizome scales of these genera are clathrate at least some parts.

Rhizome scales can divided into 3 types based on its clathrate appearance as following: (I) scale clathrate with central opaque region (this scale type has dark brown to black central opaque region while the marginal region is clathate or not clathate (sometimes the opaque region may form a very long and thin band or a circular area) (Figure 3.2A)), (II) scale clathrate and homogeneous throughout (this scale type has clathrate throughout and at different part of scale the thickness of wall between adjacent cells are not different (Figure 3.2B,D,E), (III) scale clathrate and heterogeneous (this scale type has clathrate region but different part of scale the thickness of wall between adjacent cells are different (the thickness of cells in central or basal area usually is thicker than other part (Figure 3.2C,F). On the other hand, rhizome scale may be peltate (i.e. having the stalk attached to the lower surface usually at or near the centre; umbrella-shaped) (Figure 3.2C,E, pseudopeltate (i.e. the point of attachment of scale is at base, but the base of scale form auricles below the point of attachment of scale (Figure A,B,D,F) or basifixed the point of attachment of scale is at base and the scale do not form auricles below the point of attachment of scale.

The fronds of these genera are articulate to the rhizome. The stipe, shape, size, apex, base, margin and texture are high variation. Only the pedatifid lamina were found in the *Neocheiropteris* and some specimens of *Platygyria waltonii* Ching & S.K.Wu that could be used to distinguish them from the rest. However, some speciemens of *Platygyria waltonii* Ching & S.K.Wu have hastate or pedatifid lamina or have auricles at base. The large lateral vein at the base of lamina were only found in the *Neocheiropteris palmatopedata* Christ.

Sori of most species of the genera studied in the present study form a row on either side of midrib excepting for the *Neocheiropteris palmatopedata* Christ and some specimens of *Platygyria waltonii* Ching & S.K.Wu. All species of all genera studied in the present study have clathrate paraphyses covering the sori. These paraphyses usually caduceus (Figure 3.3C,D).

According to the results shown above, genus *Lepisous*, *Paragramma*, *Platygyria* and *Neocheiropteris* were more or less similar in appearance with regard to both morphological and anatomical characters. Comparison of morphology and anatomy of *Lepisous*, *Paragramma*, *Platygyria* and *Neocheiropteris* was shown in Table 3.1.

With regard to the genus *Lepisorus*, this result is mostly similar to the results reported by Zink (1993) who study morphology and anatomy of some organs of *Lepisorus*, i.e. rhizome, indument, leaf and sori. Some details of both results were similar, for example the rhizomes short- to long creeping, glaucous or not glaucous, and covered by scales; presence of phyllopodia; presence of sclerenchyma strands on rhizome; one row of sori on either side of the costa; and sori covered by paraphyses. However, some details of these characters are different, for example: (1) the three type of scales based on clathration found in the present study (the details of scale type were shown above) while Zink found only the type II, (2) he reported the presence of sclerenchyma strands on rhizome while the presence study find that these strands are absent in some species, (2) he reported the number of vascular bundles in rhizome is 5-15 and while the present study found 2-20 vacular bundles. On the other hand, Shivastana (1967) reported that the three *Lepisorus* species (i.e. *L. kashyapii* (Mehra) Mehra, *L. macrosphearus* (Bak.) Ching and *L. subrostratum* (Hook.) C. Chr.) studied had features as following: creeping and dictyostelic rhizome, rhizome and sori covered by clathrate scales, annulus having many indurate cells, numerous sclerenchyma strands scattered in ground tissue of rhizome. These characteristics are similar to the results found in the present study. The presence of lobes at base of rhizome scales of *Lepisorus* spp. was reported by Rahaman and Sen (1999). In the present study also found this character, but the present study found that most *Lepisorus* species did not have these lobes. In adition, the result obtained from the present study is similar to the result of Yu and Lin (1997a) who reported the presence of sclerenchyma strands in rhizome of *Lepisorus* spp.

Genus *Paragramma* was maintained as distinct genus by Ching (1940), Copeland, (1947), Pichi Sermolli (1977) while Holttum (1955), Tagawa and Iwatsuki (1989), Hennipman et al. (1990) and Hovenkamp (1998a, c) recognized the combining of the *Paragramma* with *Lepisorus* s.str. The key characters that Copeland (1947) used to distinguish *Paragramma* from his *Pleopeltis* s.l. (i.e. including *Lepisorus* sens.str.) were the combination of the soral shape and the presence of lamina scales. In Copeland’s key to the genera of the Polypodiaceae, or in his description, he showed that *Paragramma* had elongated, oblong or linear-oblong sori and that its lamina was not covered by peltate scales, while his *Pleopeltis* s.l. generally had both round or elongate sori or sori fused, but the elongate sori species had peltate scales on the lamina. The findings of the present study indicate that *Paragramma longifolia* T.

Moore and *Paragramma balteiformis* Brause had round sori mixed with elongate sori. *Paragramma longifolia* T. Moore, however, had glabrous laminas while the laminas of *Paragramma balteiformis* Brause were covered by few clathrate scales. Moreover, both elongate sori and few scales on the lower surface of lamina could have occurred in some *Lepisorus* sens.str. species, i.e. *L. angustus* Ching, *L. subconfluens* Ching and *L. scolopendrium* Tagawa. Accordingly, these determined that the combining of lamina scales and sorus shape could not be used to separate *Paragramma* from *Pleopeltis* s.l.. In addition, the present study could not find any characters that can distinguish the *Paragramma* and *Lepisorus* sens.str. Therefore, based on the details shown above, the circumscription of genus *Lepisorus* should include the *Paragramma*. This summary is supported by Holttum (1955), Tagawa and Iwatsuki (1989), Hennipman et al. (1990) and Hovenkamp (1998a, c).

With regard to the genus *Neocheiropteris*, Ching (1933), and Tagawa and Iwatsuki (1989) stressed the important of tufts of hairs that dorsally attached to the rhizome scales as diagnostic character of *Neocheiropteris* s.l. The present examinations of this characteristic found that these hairs could be found in all *Neocheiropteris* spp. and *P. waltonii* Ching & S.K. Wu, but they were not found in the other *Platygyria* spp. In addition, they could be found in some *Lepisorus* species, i.e. *L. kawakami* Tagawa, *L. macrosphaerus* Ching, *L. marginatus* Ching and *L. monilisorus* (Hayata) Tagawa. Thus, this character should not be served as a key character of *Neocheiropteris*. Moreover, however the pedatifid lamina could be found in *Neocheiropteris palmatopedata* Christ and some specimens of *Platygyria waltonii* Ching & S.K. Wu, but entire lamina margin could be found in some *Platygyria* species. Accordingly, this character could not be used as a defining character for merging genus *Neocheiropteris* and the *Platygyria*. The characters can be used to distinguish all *Platygyria* species from the others were: indurate cells absent or few; stomium position was inconstant; annulus was extremely broad. From the observation in *Platygyria* Ching & S.K. Wu in comparison with the type species of *Neocheiropteris*, *Lepisorus* s.str. and *Paragramma*, it was found that the annulus characters were not only important in separating *Platygyria* from *Neocheiropteris*, but also from the *Lepisorus* s.str. and *Paragramma*. Therefore, based on the details shown above, the *Platygyria* should be classified as a distinct taxon form the *Lepisorus* sens.str., *Neocheiropteris* and *Paragramma*. This conclusion is supported by Ching & S.K. Wu (1980) and Zhang et al.(2003).

The *Neocheiropteris normallis* (D. Don) Ching was only *Neocheiropteris* species that was distinct from the rest of the *Neocheiropteris* because it had a single row of sori between midrib and the lamina margin while other *Neocheiropteris* spp. had more than 1 row of sori between midrib and the lamina margin. On the other hand, most morphological and anatomical characters of the *Neocheiropteris normallis* (D.Don) Ching fall within the ranges of variations of the genus *Lepisorus*, so this species should be treated as a *Lepisorus* species.

Table 3.1 Compaprison of some morphological and anatomical characters of genus *Lepisorus*, *Paragramma*, *Platygyria* and *Neocheiropteris*.

Morphological and anatomical characters	Taxa			
	Lepisorus	*Paragramma*	*Platygyria*	*Neocheiropteris*
Rhizome forms	short- to long crerping,	short to slightly short creeping or ascending	short- to long crerping,	short- to long crerping
Rhizome surefaces	glaucous or not glaucous	glaucous or not glaucous	glaucous or not glaucous	not glaucous
Number of vascular bundle in rhizome	2-20 vascular bundles	3-28 vascular bundles	1-11 (mostly1-5) vascular bundless	5-15 vascular bundles
Number of sclerenchyma strands in rhizome	up to128 strands	up to141 strands	mostly absent or few	present or absent
Attachmant of scales	peltate or pseudopeltate or basifixed	peltate or pseudopeltate or basifixed	peltate or pseudopeltate or basifixed	Basifixed or pseudopeltate
Clathrate appearance of rhizome	type I, II, III	II	II	III
Colour of rhizome scales	concolourous or discolourous	concolourous	concolourous	concolourous or discoloruos

Table 3.1 (Continued)

Morphological and anatomical characters	Taxa			
	Lepisorus	*Paragramma*	*Platygyria*	*Neocheiropteris*
Margin of rhizome scales	entire or erose to denticulate or dentate, sometime form long spine like teeth	denticulate or dentate with short to long spine like teeth	denticulate or dentate with short to long spine like teeth	denticulate or dentate with short to long spine like teeth
Presence of central opaque part	present or absent	absent	absent	absent
Hairs on scale	present or absent	absent	present or absent	present
Lobes near base of rhizome scale	2-3 lobes or absent	absent	absent	present or absent
Lamina scales	present or absent	present or absent	present or absent	absent
Lamina margin	entire or slightly sinuate	entire or slightly sinuate	entire, slightly sinuate, auriculate, hastate or pedatifid	entire, pedatifid
Large lateral vein at lamina base	absent	absent	absent	present or absent

Table 3.1 (Continued)

Morphological and anatomical characters	Taxa			
	Lepisorus	*Paragramma*	*Platygyria*	*Neocheiropteris*
Number of row of sori between the midrib and the lamina margin.	1	1	1 or more than one	one or more than one
Shape of sporangium	orbicular, elliptic or ovate	orbicular, elliptic or ovate	mostly globose	orbicular or ovate
Indurate celle of annulus	many	many	absent or few	many
Stomium position	between the thin wall epi- and hypostomium	between the thin wall epi- and hypostomium	not constant	between the thin wall epi- and hypostomium

3.4 Conclusion

The examination of morphological and anatomical characters of *Lepisorus* (J. Sm.) Ching sens.str., *Paragramma* T. Moore, *Platygyria* Ching & S.K.Wu and *Neocheiropteris* Christ found that some characters could be used to distinguish these genera and the cirumscriptions of these genera should be as following:

1. The circumscription of genus *Lepisorus* should include the *Paragramma* and *Neocheiropteris normalis* Tagawa because most characters of them are overlapped and they shared the following characters: (1) one row of sori between midrib and lamina margin, (2) indurate cells of annulus many, (3) the position of stomium was between the epi- and hypostomium, (3) the annulus was not very broad.

2. The *Platygyria* should be treated as a distinct taxon because it could be distinguished from both the *Lepisorus* s.l. and *Neocheiropteris*. The characters, i.e. indurate cells absent or few; inconstant position of stomium; extremely broad annulus.

3. The *Neocheiropteris* should be treated as a distinct taxon because it could be distinguished from the rest taxa by having more than 1 row of sori between midrib and lamina margin, and the following characters: (1) indurate cells of annulus many, (3) the position of stomium was between the epi- and hypostomium, (3) the annulus was not very broad.

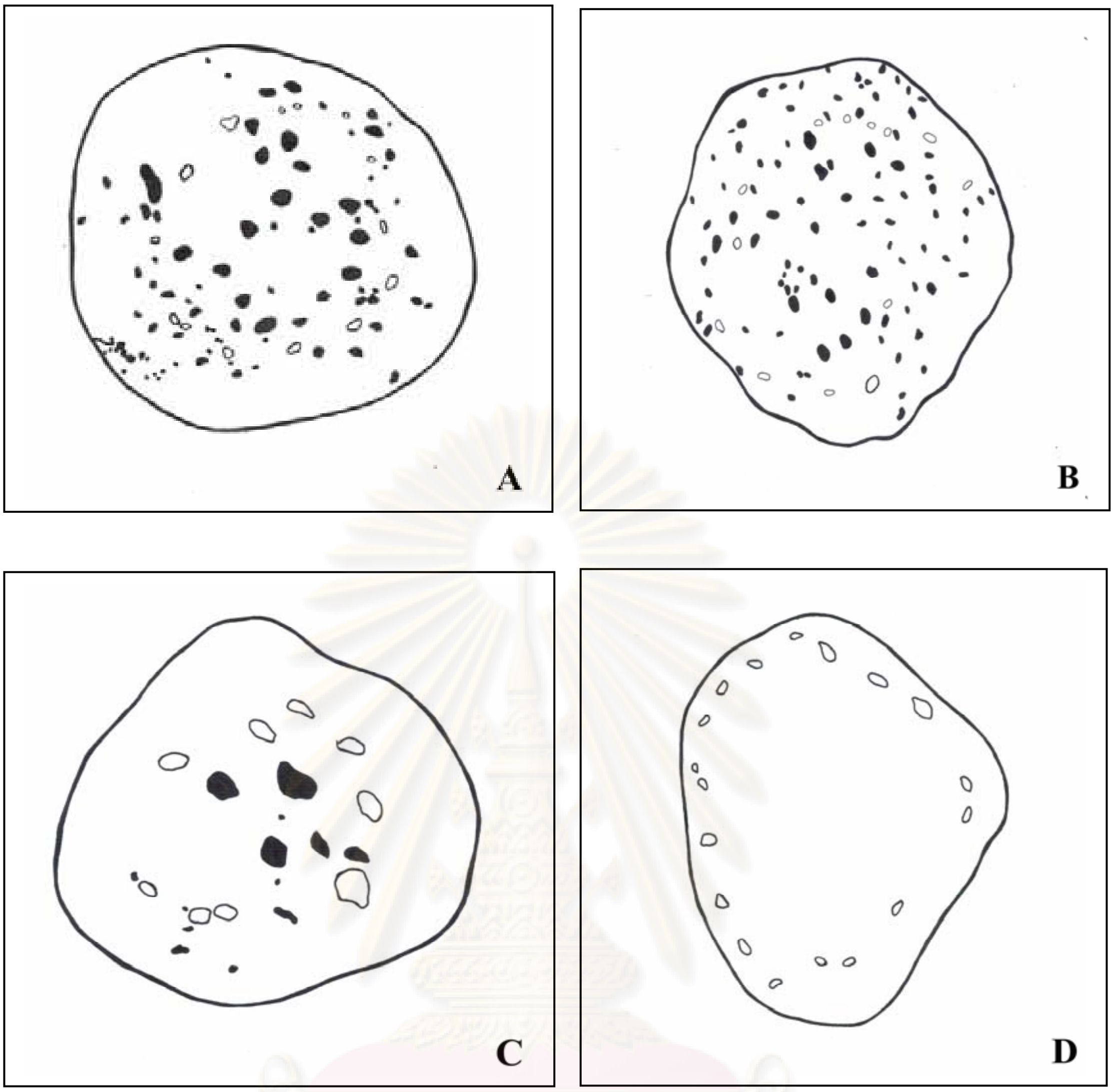

Figure 3.1 Rhizome anatomy of *Lepisorus*, *Paragramma* and *Platygyria* and *Neocheiropteris*. A. *Lepisorus scolopendrium* (Ching) Mehra & Bir (Chatan W. 410), rhizome dictyostelic with many scattered black sclenchyma strands, X60. B. *Paragramma longifolia* (Blume) T. Moore (Copeland 1585), rhizome dictyostelic with many scattered black sclenchyma strands, X60. C. *Platygyria variabilis* Ching & S.K. Wu (T.T. Yu 1239), rhizome dictyostelic with a few black sclenchyma strands, X80. D. *Neocheiropteris palmatopedata* Christ, rhizome dictyostelic without black sclenchyma strands, X80.

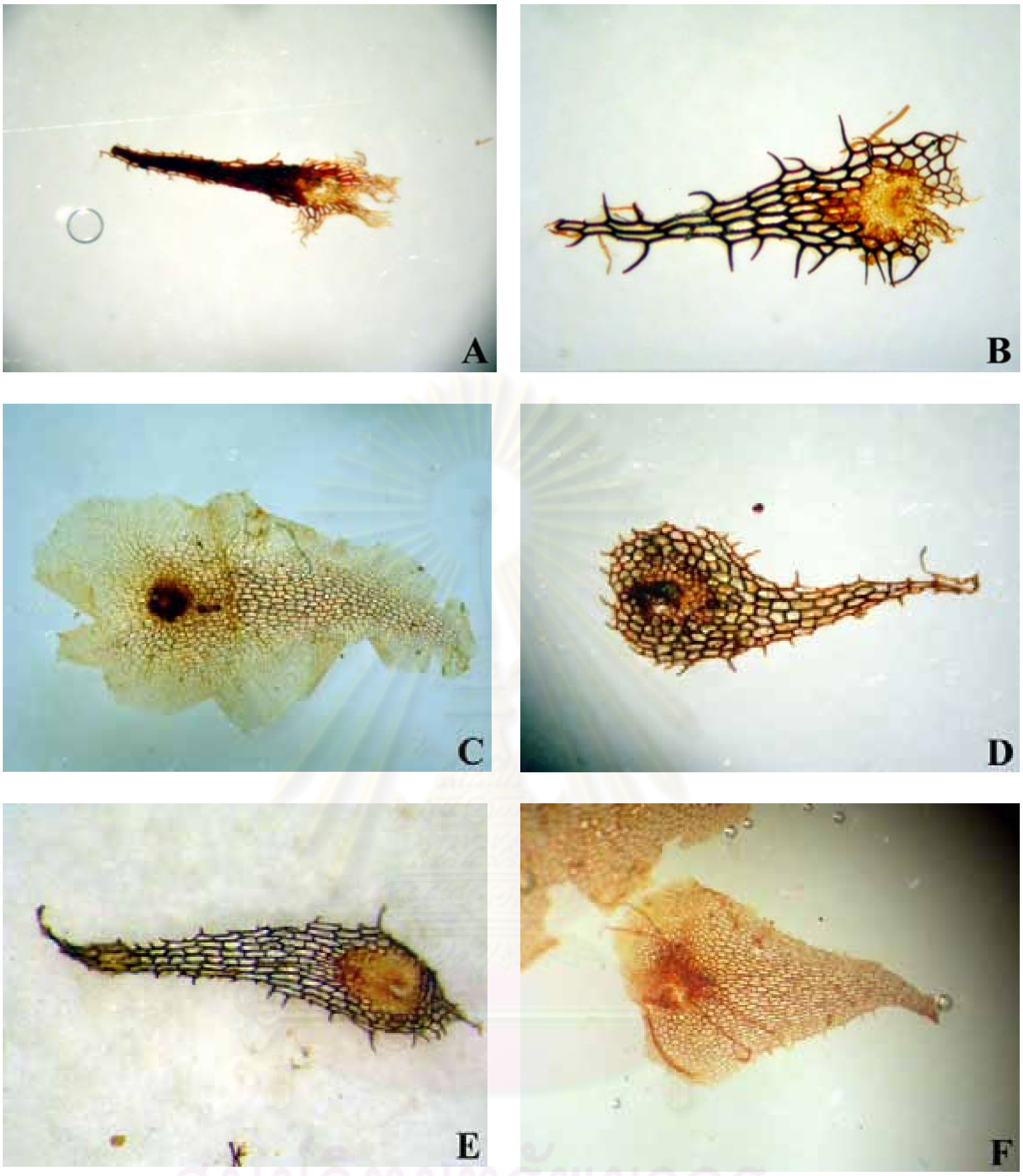

Figure 3.2 Rhizome scales of *Lepisorus*, *Paragramma* and *Platygyria* and *Neocheiropteris*. A. *Lepisorus oligolepidus* (Baker) Ching (Hennry 2049), scale pseudopeltate, clathrate with central opaque region, X100. B. *L. pseudonudus* Ching (Blanford 354), scale pseudopeltate, clathrate and homogeneous throughout, X80. C. *L. kuchenensis* (Y.C. Wu) Ching (Poilane 17045), scale peltate, clathrate and heterogeneous, X80. D. *Paragramma longifolia* (Blume) T. Moore (Matthew s.n.), scale pseudopeltate, clathrate and homogeneous throughout, X100. E. *Platygyria waltonii* (Ching) Ching & S.K. Wu, (Walton s.n.), scale peltate, clathrate and homogeneous throughout, X100. F. *Neocheiropteris palmatopedata* Christ, (Maire s.n.), scale pseudopeltate, clathrate and heterogeneous, hairy on dorsal surface, X80.

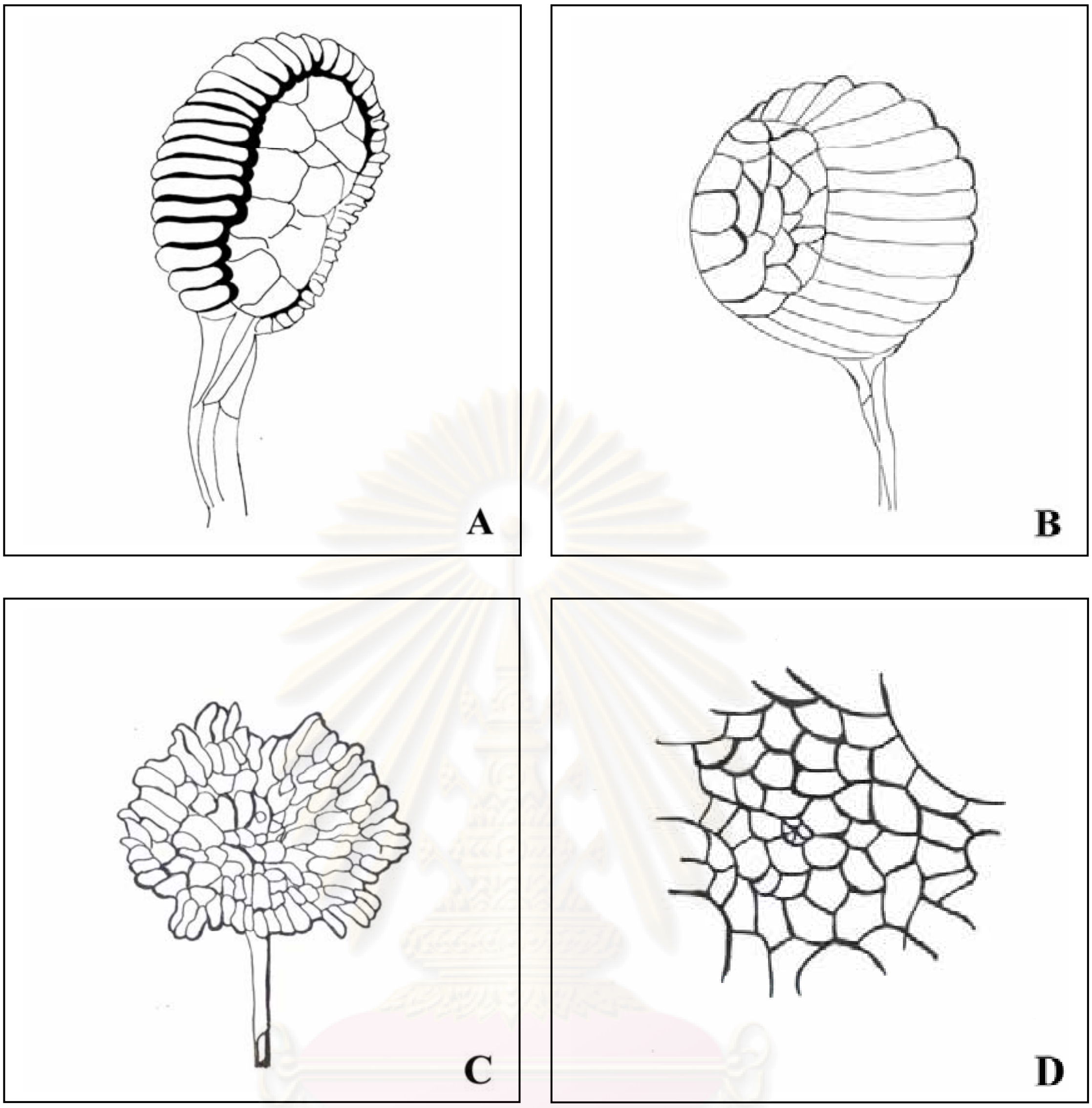

Figure 3.3 Sporangia and clathrate papaphyses of some species studied. A. *Lepisorus nudus* (Hook.) Ching (Chatan W. 466, sporangium with narrow annulus with many indurate cells, x100. B. *Platygyria waltonii* (Ching) Ching & S.K. Wu (Walton s.n.), sporangium with broad annulus, without indurate cell, x100. C. *L. nudus* (Hook.) Ching (Chatan W. 466), clathrate paraphysis, x50. D. *P. waltonii* (Ching) Ching & S.K. Wu (Walton s.n.), clathrate paraphysis, x60.

CHAPTER IV

PHENETIC RELATIONSHIPS

4.1 Introduction

In biology "phenetics" is also know as a part of numerical taxonomy that is an important developing branch of taxonomy, which received a great impetus with the development and advancement of computers (Singh, 2004). The modern methods of numerical taxonomy had their beginning from the contribution of Sneath (1957), Michener and Sokal (1957), and Sokal and Michener (1958). In addition, Sokal and Sneath (1963) published their important book for a numerical taxonomy named "Principles of Numerical Taxonomy" and then an expended and updated book was published by Sneath and Sokal (1973) known as "Numerical Taxonomy".

Sneath and Sokal (1973) defined that "numerical taxonomy is the grouping methods of taxonomic units into taxa on the a basis of their characters states, and the term includes the drawing of phylogenetic inferences from the data by statistical or other mathermatical methods to the extent to which this is possible. This method requires the conversion of information from taxonomic entities into numerical quantities". In addition, their fundamental position of numerical taxonomy, that exactly modified from Sneath (1958), were summarized in 7 principles as shown below:

1. The greater content of information in the taxa of a classification and the more characters on which it is based, the better a given classification will be.
2. A priori, every characters is of equal weight in creating natural taxa.
3. Overall similarities between any two entities is a function of their individual similarities in each of the many characters in which they are being compared.
4. Distinct taxa can be recognized because correlations of characters differ in the groups of organism under study.
5. Phylogenetic inferences can be made from the taxonomic structures of a group and from character correlations, given certain assumptions about evolutionary pathways and mechanisms.

6. Taxonomy is viewed and practiced as an empirical science.
7. Classifications are based on phenetic similarities.

Therefore, the definition made by Sneath and Sokal (1973) is viewed in the broad sense that included both phenetic and phylogenetic approaches. Generally, the two approaches were different in that in the phenetic approach, classification of organisms was based on an overall similarities while in phylogenetics, the classification was based on phylogenetic relationships. Duncan and Baum (1981) also supported numerical taxonomy in broad view. In addition, They gave the important nature of phenetics that is the use of patterns of similarity among organisms in all available characters without: (1) considering the evolutionary events that produced the observed similarity and (2) a priori weighting of the characters for the estimation of relationship and formulation of classifications.

As shown by Sneath and Sokal (1973), the details of major advantages of numerical taxonomy in systematic study include:

1. Numerical taxonomy has the power to integrate data from various sources, such as morphology, physiology, chemistry, affinities between DNA strands, amino acid sequence of proteins, and more. This is very difficult to do by conventional taxonomy.
2. Though the automation of large portions of the taxonomic process, greater efficiency is promoted. Thus, taxonomic work can be done by less highly skilled workers.
3. The data coded in numerical form can be integrated with existing electronic data processing systems in taxonomic institutions and used for the creation of descriptions, keys, catalogs, maps, and other documents.
4. Being quantitative, methods provide greater discrimination along the spectrum of taxonomic differences and are more sensitive in delimiting taxa. Thus they should give better classifications and key than the output obtaining from the conventional methods.
5. The creation of explicit data table for numerical taxonomy has already forced workers in this field to use more and better-described characters. This necessarily will improve the quality of conventional taxonomy as well.
6. A fundamental advantages of numerical taxonomy has been the reexamination of the principles of taxonomy and the purposes of classification.
7. Numerical taxonomy has led to reinterpretation of a number of biological concepts and to pose the new biological and evolutionary questions.

Formerly, both approaches of numerical taxonomy has ever been used to explore relationships, including clarifying their taxonomic problems, of various organisms. Some details of using numerical taxonomy in botanical systematics and its application were shown in Duncan and Baum (1981). In addition, publications that used numerical taxonomy to biological systematics were listed in Sneath and Sokal (1973).

4.1.1 Chapter Aims

As previously mentioned in Chapter I and II, so far there has been no taxonomic study aimed at clarifying the problem of circumscriptions for the *Lepisorus*, *Paragramma* and *Platygyria*. Therefore, the objectives of the present work were to investigate the phenetic relationship and determine the suitability of the generic circumscriptions of *Lepisorus* and the other two related genera, i.e. *Paragramma* and *Platygyria*.

With the aforementioned objectives in mind, both cluster analysis (CA) and discriminant analysis (DA) were performed based on both qualitative and quantitative characters of the herbarium specimens.

4.2 Materials and Methods

4.2.1 Plant materials

In the present study, about 2,500 herbarium specimens from around the world remaining in the herbaria in Europe (BM, E, L, K and P) and Asia (BKF, BK, PE, KUN, PYU and TI) were studied. The total number of complete specimens selected for examination comprised 516 specimens (appendix 1) which constituted the OTUs (Operational Taxonomic Units). The specimens that were included in this study belonged to *Lepisorus* sens.str. (36 species) and its related genera, i.e. *Paragramma* (1 species) and *Platygyria* (4 species). These specimens included specimens of the type species of each genus. Most of these specimens were identified by examining type specimens whereas the others were specimens determined by Bir and Trikha (1969) or M. J. Zink (i.e. determined on herbarium sheets) or Ching (1933) or Zhang et al. (2003), or identifications were made by consulting literature, i.e. Ching (1933), Hovenkamp (1998a, c), Zink (1993), Shieh et al. (1994), Verdcourt (2001), Tagawa and Iwatsuki (1989) and Zhang et al. (2003).

In order to determine the taxonomic position of *Platygyria* the specimens of *Neocheiropteris ensata* Ching *Neocheiropteris normalis* Tagawa and *Neocheiropteris palmatopedata* Christ (i.e. the type species of the *Neocheiropteris*) were also included in these analyses and they were treated as the representatives of the genus.

For the purposes of this study, *Pleopeltis* sens.str. Humb. et Bolpl. ex Willd. was excluded because it differs from *Lepisorus* sens.str. in both morphology and anatomy. The distinctions of them were detailed by Zink (1988, 1993) and Rahaman and Sen (1999). Although some pteridologists, i.e. Copeland (1947) and Pichi Sermolli (1977) combined them together, most recent taxonomic treatments, i.e. Hennipman et al. (1990), Andrews and Windham (1993), Zink (1993), Hovenkamp (1998a, c), Verdcourt (2001), Mickel and Smith (2004), Smith et al. (2006) etc, have agreed to keep them separate. Moreover, the consent to keep them as separated taxa has been supported by molecular systematic study (Schneider et al., 2004).

4.2.2 Morphological and anatomical characters

Fifty-six morphological and anatomical characters were examined for each of the 516 specimens. Measurement was carried out by using a Keiba digital caliper No. 111-101HB or specimens were measured under Zeiss stereo (Stemi DV4) and Olympus light (CH30) microscopes. Of these characters, twenty-six were quantitative including four ratio characters, and twenty-seven were qualitative characters scored as binary or multi-state characters. The characters used in this study are shown in Table 4.1 These characters and their states were used to construct a data matrix.

4.2.3 Phenetic analysis

The phenetic relationships were investigated by two types of multivariate analysis, i.e. cluster analysis (CA) and discriminant analysis (DA). The CA was performed by using an unweighted pair-group method with arithmetic averages (UPGMA) clustering implemented in the Multivariate Statistical Package (MVSP), Version 3.13 (Kovack Computing Services) to place the individual specimen into groups. Because the characters submitted to analysis were both quantitative and qualitative, the Gower similarity coefficient (GSC) (Gower, 1971) was calculated and clustered by the group-average method of the MPSV program while the details of the suitability of GSC for analysis based on mixed characters was shown by St-Laurent and Baum (2000). The characters used in the analyses were assumed to be equal in importance and unweighted.

A subset of characters that maximized differences among the groups determined by CA or other groups (i.e. the *Lepisorus* sens.str., *Paragramma*, *Platygyria* and also the *Neocheiropteris*) that were recognized by previous pteridologists as a distinct group were selected by stepwise discriminant analysis. Prior to performing discriminant analyses, the data matrix was modified, i.e. characters that did not satisfy the assumption of normal distribution were transformed by taking them with the natural logarithm. To characterize the mean differences among species, canonical discriminant analysis was used to acquire insight into group differences and estimate character weights from correlations between canonical variables and original variables. The canonical discriminant analyses was performed by using the CLASSIFY procedure in SPSS/PC for Windows, release 10.0 (Anonymous, 1999).

Table 4.1 List of twenty-six quantitative and twenty-seven qualitative characters with unit or character states used in the study of the *Lepisorus* and its related genera.

Abbreviation	Characters
RHS	rhizome surface: not glaucous (0), glaucous or not glaucous (1), glaucous (2)
RHDM	rhizome diameter in mm
RHSI	shortest rhizome internode length in mm
RHLI	longest rhizome internode length in mm
NM	number of meristele in rhizome
NSSR	number of sclerenchyma strand in rhizome
RSAS	apex of rhizome scale: obtuse (0), obtuse or acute (1), acute or acuminate, and not obtuse (2), filiform (3)
RSBS	base of rhizome scale : obtuse or round (0), obtuse or round or cordate (1), cordate (2)
RSM	margin of rhizome scale: entire (0), entire, or dentate or denticulate (1), dentate or denticulate(2)
RSS	shape of rhizome scale: lanceolate or triangular or ovate(0), circular or lanceolate or triangular or ovate (1)
RSCL	clathrate appearance of rhizome scale: clathrate thoughout (0), center clathrate with not clathate margin (1), center clathrate with not clathrate margin, or center opaque with clathrate or not clathrate margin (2), center opaque with clathrate and not clathate margin (3)
RSLE	rhizome scale length in mm
RSWI	rhizome scale width in mm
RSOR	orientation of rhizome scale: appressed (0), appressed or slightly spreading (1), slightly spreading (2), strongly spreading (3)

Table 4.1 (continued)

Abbreviation	Characters
RSCO	rhizome scale colour: one colour (0), one or two colours (1), two colours (2)
RSAT	attachment of rhizome scale: all scale basifixed (0), pseudopeltate or basifixed or peltate (1), all scale peltate (2)
RSUS	appearance of hairs on upper surface of rhizome scale: absent (0), present (1)
RSL	lobe of rhizome scale: absent (0), present (1)
RSIP	insertion point of rhizome scale: at base or close to base more than apex (0), at base or at the middle or close to base more than apex (1)
STL	stipe length in mm
STD	stipe diameter at the middle of its length in mm
PHL	phyllopodia length in mm
PHD	phyllopodia diameter in mm
LI	lamina indentation : margin entire or slightly waved (0), auriculate (1), hastate or pedatifid (2)
LA	lamina apex: acute (0), acute or acuminate (1), acute or acuminate or obtuse or round (2), acute or obtuse or round (3), acuminate (4), acuminate or obtuse or round (5), obtuse or round (6)
LL	lamina length in mm
LW	lamina width in mm
LT	lamina texture: membranaceous or chartaceous (0), membranaceous to coriaceous (1), subcoriaceous to coriaceous (2)
ABL	abaxial surface of lamina: lamina glabrous (0), lamina covered by few to low density of scales near the base or near midrib or on midrib (1)

Table 4.1 (continued)

Abbreviation	Characters
ADL	adaxial surface of lamina: lamina glabrous (0), lamina glabous or covered by few to moderate density of scales near lamina base or near midrib or on midrib (1)
LPL	longitudinal posture of lamina margin: flat (0), slightly revolute(1), strongly revolute (2)
LV	veins or lateral vein prominence on abaxial surface of lamina: inconspicuous (0), inconspicuous and conspicuous (1), conspicuous (2)
LASL	length of the apical sterile portion of lamina in mm
LBS	symmetry of lamina base: symmetric or nearly symmetric (0), present both symmetric and asymmetric base (1)
SL	sorus length in mm
BSW	sorus width in mm
SODBA	sori distribution between lamina base and apex: only on upper half (0), on upper half or reaching to the lower half (1); only on lower half (2)
SORN	sorus row number between midrib or rachis, and the margin: one row (0), one row or more than one row (1), more than one row (2)
SOPO	sorus position between midrib and margin: only at the middle (0) between middle and midrib (1); between middle and margin (2), close to midrib to close to the margin (3), only close to the midrib (4); only close to the margin (5)
LFPL	length of the fertile portion of lamina in mm

Table 4.1 (continued)

Abbreviation	**Characters**
SOR	sori orientaion when compare with the closest midrib: not oblique (0), present both oblique and not oblique sori (1), oblique (2)
SPOL	sporangium length in µm
SPOW	sporangium width in µm
AW	annulus width in µm
STOP	stomium position: at the position between the thin wall epi- and hypostomium (0), not constantly positioned on annulus (1)
SPL	spore length in µm
SPW	spore width in µm
INDC	occurrence of indurate cells: many (0), absent or few (1)
STPH	ratio of stipe length and phyllopodium length
LLST	ratio of lamina length and stipe length
LLLT	ratio of lamina length and lamina tip length
LLLA	ratio of lamina length and length of sori occurred area
BALV	large lateral vein at lamina base: absent (0), present (1)

4.3 Results and Discussion

4.3.1 Cluster analysis

The UPGMA dendrogram that constructed using Gower similarity coefficient measure for the combined data of both quantitative and qualitative characters of all OTUs in the present study showed three discrete groups (Fig. 4.1), at the Gower similarity coefficient 0.76. Group 1 comprised *Neocheiropteris* and Group 2 comprised *Platygyria*. In addition, Group 3 was the largest group composed by combining *Lepisorus* s.s and *Paragramma*. At Gower similarity coefficient 0.72, these ferns were divided into two groups, i.e group 1 and a group composed of group 2 and 3 (Figure 4.1). Group 1 is distinct from the rest mainly by the combination characters of presence of large lateral veins at the lamina base, pedatifid lamina and sporangium characters as shown in the key to taxa below. These results suggested that genus *Neocheiropteris* was rather distinct from the rests while genus *Platygyria* was more closely related to genus *Lepisorus* and *Paragramma*. In addition, genus *Lepisorus* and *Paragramma* is very closely related to each other than to other taxa.

4.3.2. Canonical Discriminant Analysis

This analysis was divided into two analyses based on the number of prior groups obtained: (1) four groups, including *Lepisorus* sens.str., *Neocheiropteris*, *Paragramma* and *Platygyria*, all of which were assigned based on the treatments of previous pteridologists who acknowledged them as distinct taxon in relation to one another, (2) three groups, including groups 1, 2 and 3, which were obtained by previous CA. Overall, twenty-six quantitative characters were used in these analyses with a purpose to test their groupings. Once the stepwise analysis had been performed for all four groups, the linear discriminant function classification showed that 96.9% of the specimens had been correctly classified . The nature of the differences between the entries were shown by the pooled within canonical structure (Table 4.2) wherein canonical variable 1 was 97.3% correlated with the twenty-six characters and explained 87.6% of the total variance, which was highly associated with the AW, NM. Canonical variable 2 was 79.6% correlated with the twenty-six characters and explained 8.5% of the total variance, which was highly associated with characters LW, PHD, STL, SW, SL, SPOW, RSWI. Canonical variable 3 was 66.7% correlated with the twenty-six characters and explained 3.9% of the total variance, which was highly associated with the NSSR, PHL, RHLI, LLLA, SPW while the RHDM, LLST, LFPL, STD, STPH, LL, LASL, SPOL, RHSI, SPL, LLLT, RSLE were not selected by stepwise discriminant analysis to be used in further canonical discriminant analysis. The summary of canonical discriminant function of 4 categories based on 26 morphological and anatomical characters was shown in Table 4.4.

The stepwise analysis was carried out for the three groups, i.e. these groups were split by the UPGMA dendrogram at Gower similarity coefficient = 0.76. The most 12 important characters for separating these taxa were AW, SPOL, LFPL, LW, LLST, SL, STPH, LLLT, SPL, NSSR, SPOW and SW. The F-value, means and standard errors of the 26 quantitative characters for the three groups were shown in Table 4.5. The nature of the differences between the entries was shown by the pooled within the canonical structure (Table 4.6) wherein canonical variable 1 was 97.2% correlated with the twenty-six characters and explained 90.7% of the total variance, which was highly associated with the characters AW, SPOL and LFPL. Canonical variable 2 was 79.9% correlated with the twenty-six characters and explained 9.3% of the total variance which was highly associated with the characters LW, LLST, SL, STPH, LLLT, SPL, NSSR, SPOW and SW while the characters excluded from the analysis were LLLA, LL, NM, STL, LASL, PHD, RHLI, RHDM, RSWI, STD, SPW, RHSI, RSLE and PHL. The linear discriminant function classification (Table 4.7) showed that the specimens had been 100% correctly classified; obviously, therefore, this function could be used for further identification of these ferns. The summary of canonical discriminant function of 3 categories based on 26 morphological and anatomical characters was shown in Table 4.8.

The ordination plot on the two canonical axes obtained from the four groups analysis (Fig. 2A) showed that canonical axis 1 divided these plants into two groups, i.e. one group including *Lepisorus* sens.str., *Paragramma* and *Neocheiropteris*, and the other consisting solely of the *Platygyria* while the canonical axis 2 could not divide these ferns. The ordination plot on the two canonical axes obtained from the three groups analysis (Fig. 2B) revealed that canonical axis 1 divided these plants into two groups, i.e. one group including *Lepisorus* sens.str., *Paragramma* and *Neocheiropteris*, and the other consisting solely of the *Platygyria*. However, canonical axis 2 was able to separate the *Neocheiropteris* from the rest.

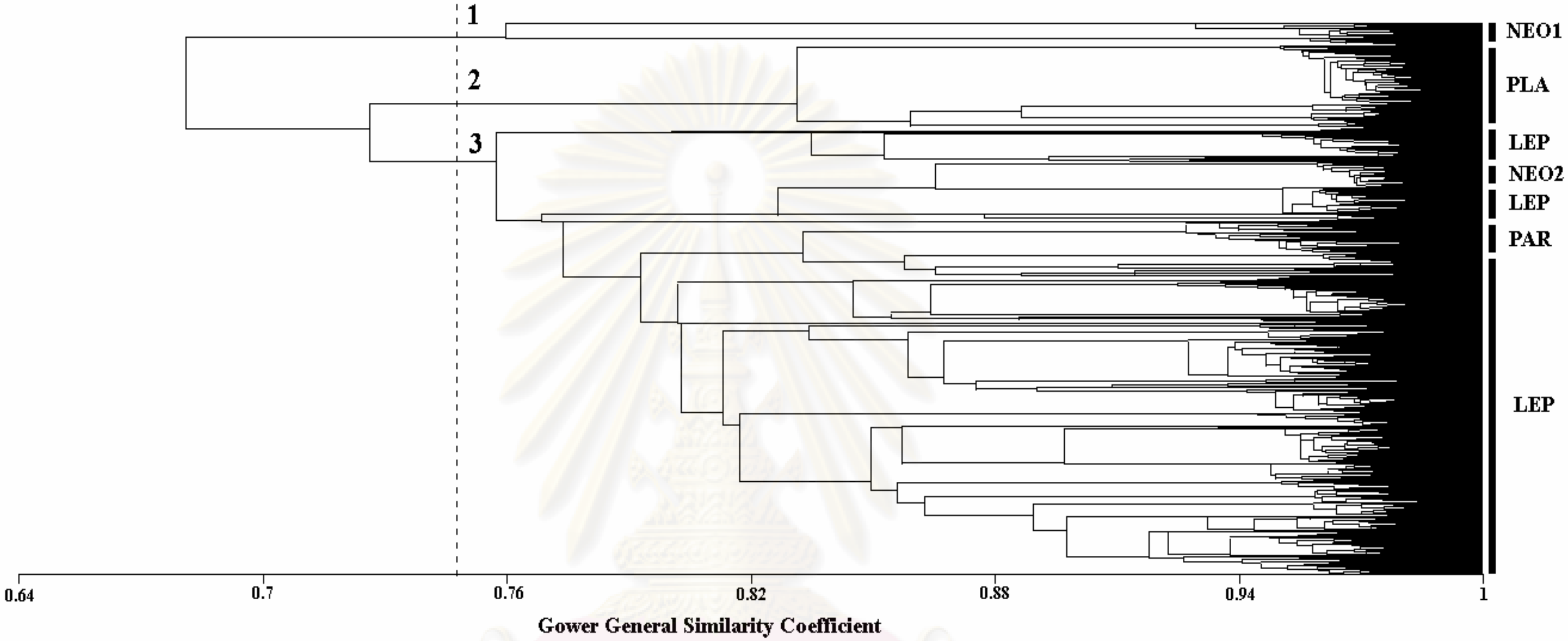

Figure 4.1 UPGMA clustering of 516 OTUs based on 53 quantitative and qualitative characters of the *Lepisorus*, *Paragramma*, *Platygyria* and *Neocheiropteris* (LEP= *Lepisorus*, PAR= *Paragramma*, PLA= *Platygyria*, NEO= *Neocheiropteris*).

Table 4.2 Pooled within canonical structure of the four priori groups (i.e. *Lepisorus*, *Paragramma*, *Platygyria* and *Neocheiropteris*) as recognized by pteridologists, results based on 26 quantitative characters scored in this study. Characters in bold were selected by stepwise discriminant analysis for further use in canonical discriminant analysis. * the most highly associated between each variable and any discriminant function.

Characters	Discriminant function		
	1	2	3
AW	0.957*	0.041	-0.018
NM	-0.083*	0.083	-0.055
LW	-0.018	0.467*	-0.120
PHD	-0.097	0.395*	0.202
STL	0.019	0.329*	0.017
RHDM	-0.038	0.237	0.031
LLST	0.053	0.227	0.019
SW	0.002	-0.221*	-0.080
LFPL	-0.076	0.202	0.187
STD	-0.084	0.198	0.181
SL	-0.010	0.193*	0.166
STPH	-0.045	-0.192	0.160
SPOW	0.087	0.191*	-0.016
LL	-0.061	0.169	-0.003
LASL	-0.032	0.159	-0.139
SPOL	0.004	0.109	0.008
RSWI	0.002	0.090*	-0.087
NSSR	-0.081	-0.115	0.531*
PHL	-0.052	0.264	0.345*
RHLI	-0.098	0.292	-0.339*
LLLA	0.026	0.100	0.245*
SPW	0.123	-0.166	0.223*
RHSI	-0.019	0.152	-0.171
SPL	0.072	-0.077	0.154
LLLT	0.008	0.042	-0.128
RSLE	0.089	-0.002	-0.106

Table 4.3 Classification Function Coefficients of four groups (i.e. *Lepisorus*, *Paragramma*, *Platygyria* and *Neocheiropteris*) obtained from CA based on the 26 quantitative characters.

Characters	Categories			
	1	2	3	4
RHLI	4.481	0.565	2.095	1.154
NM	17.216	16.313	17.312	13.843
NSSR	-0.139	-0.100	-0.060	0.038
RSWI	-13.353	-8.361	-10.935	-13.643
STL	3.841	5.621	3.516	3.217
PHL	-6.830	-3.806	-5.793	-1.996
PHD	-5.606	-11.956	-8.835	-4.123
LW	9.241	3.677	4.386	4.856
SL	14.524	7.835	9.330	15.359
SW	-6.666	-2.413	-1.685	-5.662
SPOW	0.218	0.234	0.186	0.206
AW	0.266	1.326	0.343	0.371
SPW	0.880	1.155	1.008	1.067
LLLA	2.524	1.640	1.367	3.849
(Constant)	-105.484	-214.844	-85.688	-97.634

Table 4.4 Summary of canonical discriminant function of 4 categories based on 26 morphological and anatomical characters

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation	Wilks' Lambda	Chi-square	df	Sig.
1	17.872	87.6	87.6	0.973	0.011	2283.084	42	0.000
2	1.727	8.5	96.1	0.796	0.203	802.503	26	0.000
3	0.802	3.9	100.0	0.667	0.555	296.841	12	0.000

Table 4.5 F-values, means and standard errors of 26 quantitative characters of three groups (i.e. *Lepisorus* (including *Paragramma*), *Platygyria* and *Neocheiropteris* (LEP= *Lepisorus*, PAR= *Paragramma*, PLA= *Platygyria*, NEO= *Neocheiropteris*).

Characters	F-value	Sig.	LEP (including PAR and NEO ensata Ching)		PLA		NEO	
			Mean	SE	Mean	SE	Mean	SE
RHDM	52.876	0.000	2.571	0.056	1.643	0.041	4.756	0.320
RHSI	27.039	0.000	3.641	0.162	1.31	0.072	8.636	1.042
RHLI	40.205	0.000	7.660	0.381	2.989	0.179	12.643	1.096
NM	31.521	0.000	9.646	0.186	6.397	0.215	11.048	0.600
NSSR	35.727	0.000	30.955	1.118	10.231	1.125	12.952	4.975
RSLE	17.615	0.000	2.635	0.065	2.92	0.046	4.035	0.333
RSWI	15.856	0.000	1.062	0.028	1.036	0.024	1.649	0.131
STL	76.052	0.000	26.800	1.293	29.719	1.781	273.542	32.379
STD	50.775	0.000	1.395	0.042	0.947	0.037	2.457	0.199
PHL	12.789	0.000	1.337	0.094	0.877	0.048	1.619	0.134
PHD	65.254	0.000	1.851	0.036	1.207	0.03	3.790	0.299
LL	43.702	0.000	232.681	6.391	106.141	4.357	274.079	21.219
LW	130.532	0.000	18.831	1.866	16.332	1.183	195.497	19.758
LASL	59.194	0.000	18.672	0.696	11.101	0.811	126.941	17.470
SL	64.556	0.000	3.879	0.071	3.771	0.095	13.086	2.428

Table 4.5 (continued).

Characters	F-value	Sig.	LEP (including PAR and NEO ensata Ching)		PLA		NEO	
			Mean	SE	Mean	SE	Mean	SE
SW	.023	0.977	2.504	0.049	2.482	0.085	2.478	0.182
LFPL	4.567	0.011	112.513	3.812	71.973	3.381	111.373	15.838
SPOL	11.572	0.000	321.272	2.773	351.859	4.12	313.040	4.726
SPOW	41.708	0.000	246.803	2.070	286.346	2.343	218.864	3.062
AW	3982.961	0.000	51.267	0.464	182.5	2.352	46.482	2.711
SPL	15.393	0.000	59.853	0.334	61.899	0.552	52.930	1.651
SPW	69.161	0.000	40.792	0.310	48.827	0.685	34.511	1.135
STPH	70.623	0.000	0.115	0.008	39.105	2.866	131.488	34.274
LLST	98.124	0.000	0.146	0.011	4.598	0.332	0.943	0.116
LLLT	36.656	0.000	0.101	0.005	12.653	0.838	1.001	0.162
LLLA	3.055	0.048	0.538	0.025	1.559	0.053	2.637	0.480

Table 4.6 Pooled within canonical structure of three groups (i.e. *Lepisorus* (including *Paragramma*), *Platygyria* and *Neocheiropteris*) obtained from CA based on 26 quantitative characters. Characters in bold were selected by stepwise discriminant analysis for further use in canonical discriminant analysis. * indicates the most highly associated between each variable and any discriminant function.

Characters	Discriminant function	
	1	2
AW	0.950*	0.019
LLLA	0.098	-0.014
LL	-0.089	-0.058
SPOL	0.051*	0.021
NM	-0.049	-0.040
LFPL	-0.032*	0.013
LW	-0.011	-0.536*
STL	0.030	-0.409
LLST	0.087	-0.378*
SL	-0.010	-0.377*
STPH	-0.053	0.359*
LASL	-0.045	-0.331
LLLT	0.017	-0.280*
PHD	-0.022	-0.237
RHLI	-0.033	-0.220
RHDM	-0.020	-0.205
RSWI	-0.033	-0.178
STD	-0.073	-0.164
SPL	0.032	0.155*
SPW	0.055	0.141
RHSI	0.006	-0.132
NSSR	-0.080	0.129
RSLE	0.065	-0.127
SPOW	0.091	0.103*
PHL	-0.037	-0.094
SW	-0.002	0.004*

Table 4.7 Classification Function Coefficients of three groups (i.e. *Lepisorus* (including *Paragramma*), *Platygyria* and *Neocheiropteris*) obtained from CA based on the 26 quantitative characters.

Characters	Categories		
	1	2	3
NSSR	-0.125	-0.089	-0.010
LW	7.342	-0.419	-0.448
SL	15.569	1.725	3.472
SW	-4.750	-1.419	-0.210
LFPL	-0.480	4.781	3.314
SPOL	0.034	0.035	0.010
SPOW	0.083	0.170	0.140
AW	0.334	1.350	0.377
SPL	1.106	1.257	1.289
STPH	-13.362	-10.280	-10.907
LLST	-9.564	-7.484	-9.982
LLLT	0.569	-0.502	-0.683
(Constant)	-114.939	-225.377	-104.973

Table 4.8 Summary of canonical discriminant function of 3 categories based on 26 morphological and anatomical characters

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation	Wilks' Lambda	Chi-square	df	Sig.
1	17.271	90.7	90.7	0.972	0.020	1983.382	24	0.000
2	1.768	9.3	100.0	0.799	0.361	514.749	11	0.000

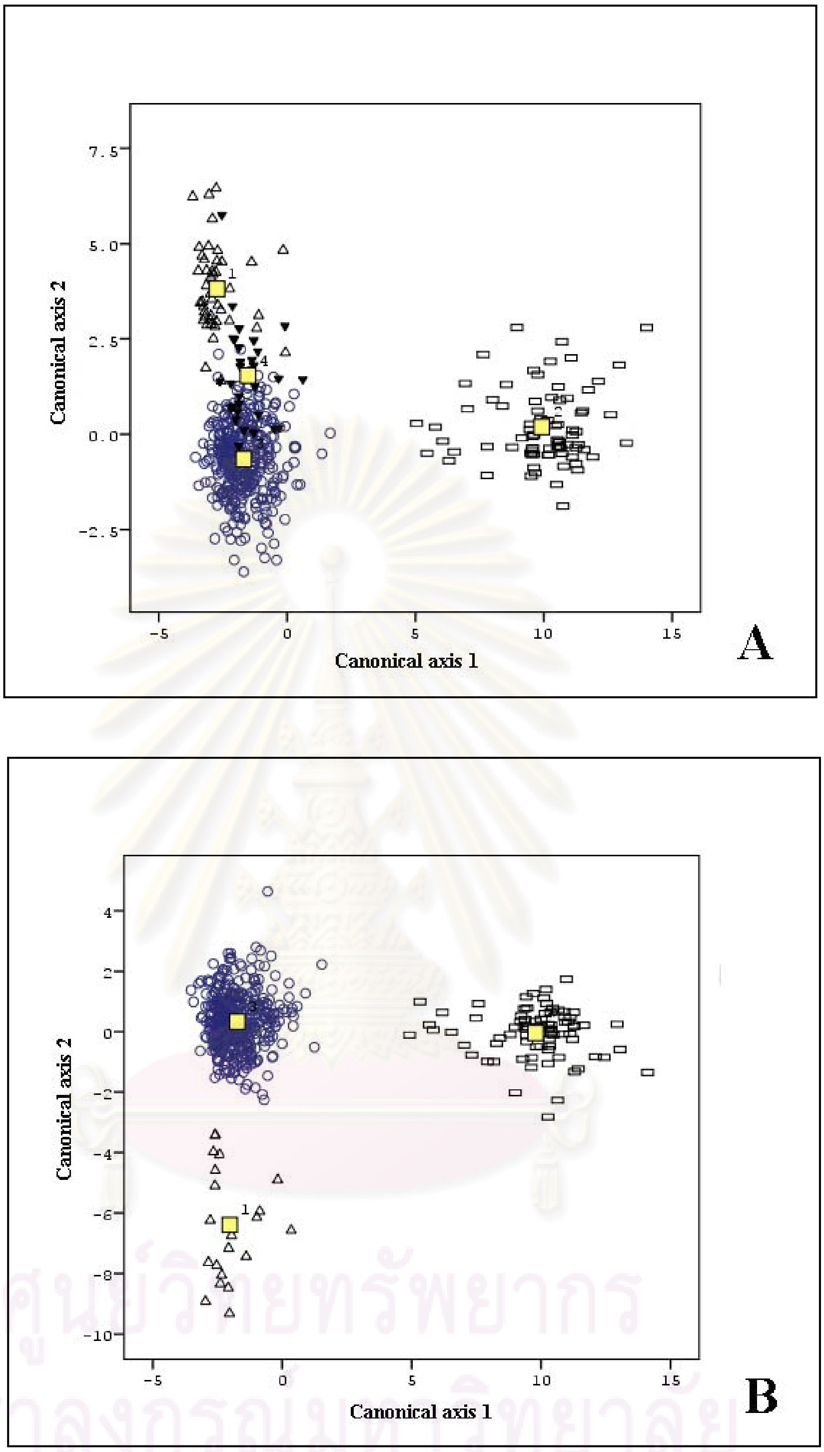

Figure 4.2 Ordination plot on the canonical axes 1 and 2. A.the ordination plot of the 4 priori assigned groups (○ = *Lepisorus*, ▼= *Paragramma*, ▭ =*Platygyria*, △= *Neocheiropteris*), B. the ordination plot of the 3 priori assigned group (○ = *Lepisorus* (including *Paragramma*, ▭ =*Platygyria*, △= *Neocheiropteris*).

4.3.3 The circumscription of *Lepisorus* sens.str. and *Paragramma* T. Moore

The results of both Cluster and Discriminant analyses showed that specimens of *Paragramma* was mixed with specimens of *Lepisorus* sens.str. (Fig. 4.1 and 4.2), this result suggests a close relationship between them. As far as the taxonomic position or circumscription of the *Paragramma* is concerned, there are two different forms of recognition thus far, i.e. the form that maintains them as a distinct genus (Ching, 1940; Copeland, 1947; Pichi Sermolli, 1977) and the form that combines the *Paragramma* p.p. with *Lepisorus* sens.str. (Holttum, 1955; Tagawa and Iwatsuki, 1989; Hennipman et al., 1990; Hovenkamp, 1998a, c). The key characters that Copeland (1947) used to distinguish *Paragramma* from his *Pleopeltis* s.l. (i.e. including *Lepisorus* sens.str.) were the combination of the soral shape and the presence of lamina scales. In Copeland's key to the genera of the Polypodiaceae, or in his description, he showed that *Paragramma* had elongated, oblong or linear-oblong sori and that its lamina was not covered by peltate scales, while his *Pleopeltis* s.l. generally had both round or elongate sori or sori fused, but the elongate sori species had peltate scales on the lamina. As the result show in Chapter 3, the findings indicate that *P. longifolia* T. Moore and *P. balteiformis* Brause had round sori mixed with elongate sori. *P. longifolia* T. Moore, however, had glabrous lamina while few clathrate scales occurred on the lamina in *P. balteiformis* Brause. Moreover, both elongate sori and few to low scale density on the lower surface of lamina could have occurred in some *Lepisorus* sens.str. species, i.e. *L. angustus* Ching, *L. subconfluens* Ching and *L. scolopendrium* Tagawa. Accordingly, these determined that the combining of lamina scales and sorus shape could not be used to separate *Paragramma* from *Lepisorus* sens.str.

In all the results of both the CA and DA analyses together with Holttum (1955), Tagawa and Iwatsuki (1989), Hennipman et al. (1990) and Hovenkamp (1998a, c) strongly supported the inclusion of the genus *Paragramma* with *Lepisorus*- in other words *Paragramma* should be treated as a synonym of *Lepisorus*. In contrast, the result of the present study disagree to divide the *Paragramma* from the *Lepisorus* as the recognition of Ching (1940), Copeland (1947) and Pichi Sermolli (1977).

4.3.4 Circumscription of *Platygyria* Ching & S.K. Wu

Firstly, *Platygyia* was proposed as a genus of Polypodiaceae by Ching and S.K. Wu (1980) wherein the characters used to define this taxon were the globose sporangium and the very broad annulus consisting of scarcely indurate cell walls. So far, three taxonomic treatments have been recognized for *Platygyria* Ching & S.K. Wu, i.e. combining with *Lepisorus* sens.str. (Yu and Lin, 1997b; Fraser-Jenkins, personal communication, 2008), treating it under *Neocheiropteris* s.l. (Ching, 1933; Hennipman et al., 1990) and maintaining the status of a distinct genus (Ching and Wu, 1980; Zhang et al., 2003). The most recent opinion of taxonomic position was proposed by Fraser-Jenkins (personal communication, 2008). He had an opinion that all *Platygyria* species should belong to *Lepisorus clathratus* (C.B.Clarke) Ching. and noted that annulus characters are not constant while Zhang et al (2003) determined that they are rather stable. From my own observation in *Platygyria* Ching & S.K. Wu in comparison with the type species of and *Lepisorus* s.l., as shown in Chapter III, it was found that the annulus characters were not only important in separating *Platygyria* from *Neocheiropteris*, but also from the *Lepisorus*. This finding indicates that all specimens or species that have globose sporangium with few or lacking indurate cells should belong to *Platygyria*.

During examining the suitable qualitative characters for cluster analysis it was found that there were two characters that clearly distinguish these genera but they have never been used as key characters in previous works. The first one is the presence of large lateral veins at the lamina base (Figure 1.5), which is the striking character of *N. pamatopedata* Christ, this character is not found in *Lepisorus* s.l. or *Platygyria* . The second character was the position of the stomium. According to Wilson (1959), the annulus was the whole ring of cells horizontally encircling the capsule and interrupted at the point of attachment to the stalk. In general, annulus comprising of a row of indurate cells interrupted by thin wall cells of epistomium, stomium and hypostomium. The stomium in most ferns usually occur between the epi- and hypostomium, but it is never found on the row of indurate cells. However, in *Platygyria*, the annulus cells are homogeneous or slightly homogeneous, and most or all annulus cells had thin walls. For these reasons, the position of the stomium in *Platygyria* is not always in a fix pattern as in the other ferns and can be found throughout or slightly throughout the annulus.

However, when herbarium specimens were examined, it was found that some specimens have globose sporangia, rather broad annulus (>100 µm) and few indurate cells or absent. They were mixed with flat or slightly flat sporangia, narrow annulus (<90 µm) and prominent indurate cells. These specimens were mixed with specimens of *Lepisorus clathratus* (C.B. Clarke) Ching and were put under *Lepisorus clathratus* complex 's cover. In my opinion, specimens that had a globose sporangia and few indurate cells of annulus (or absent) mixed with flat or slightly flat sporangia and prominent indurate cells should belong to *Platygyria*.

To sum up based on the result of both CA and DA, *Platygyria*, *Lepisorus* s.l. and *Neocheiropteris* were split into three distinct groups (Fig. 1 and 2). These phenetic results were supported by the recognition of Ching and Wu (1980), and Zhang et al. (2003) in maintaining *Platygyria* as a distinct taxon. It can be concluded that the characteristic of the *Platygyria* should be globose sporangia, very broad annulus (> 100 µm) and few indurate cells of annulus (or absent). In addition, *Platygyria* should also include the species or specimens that have globose sporangia, very broad annulus (> 100 µm) and few indurate cells of annulus (or absent) and mixed with flat or slightly flat sporangia, narrow annulus (<190 µm) and prominent indurate cells.

4.4 Conclusion

Previously, the three taxa i.e. *Lepisorus* sens.str., *Paragramma*, *Platygyria*, were recognized in a strict sense as separated genera by some pteridologists, i.e. *Lepisorus* sens.str. recognized by Ching (1933, 1940); *Paragramma* recognized by Ching (1940), Copeland (1947) and Pichi Sermolli (1977); and *Platygyria* was recognized by Ching and Wu (1980) and Zhang et al. (2003). Also, *Neocheiropteris* was recognized as a distinct genus from the genera above (Christ, 1905). From the result of morphological and anatomical studies together with the results from the two multivariate analyses. It is reasonable to conclude that *Platygyria* is a distinct taxon. While the boundary of the genus *Lepisorus* should include all member species of the genus *Paragramma*. Moreover, *Neocheiropteris* should be put to a different group; however, more specimens of the other *Neocheiropteris* species were needed to be examined.

This study found important quantitative characters that could be used to separate the genus *Lepisorus* (including *Paragramma* and *Neocheiropteris normalis* Tagawa), *Platygyria* and *Neocheiropteris*, i.e. annulus width, sporangium length, length of the fertile portion of lamina, lamina width, ratio of lamina length and stipe length, sorus length, ratio of stipe length and phyllopodia length, ratio of lamina length and lamina tip, spore length, number of sclerenchyma strand in rhizome, sporangium width and sorus width. The box plots of the six most important characters that separate these ferns are shown in Figure 4.3. The annulus width, together with some useful qualitative characters, i.e. occurrence of indurate cells and stomium position were used to construct a key to determine these 3 ferns genera.

Key to taxa

1a	Annulus width was more than 100 µm, indurate cell many,, stomium not constantly positioned on annulus...	**2. Platygyria.**
b	Annulus width less than 90 µm, indurate cell few or absent Stomium between the thin wall epi- and hypo-stomium	2
2a	Row of sori between midrib and lamina margin 1 row………	**3. Lepisorus** (including **Paragramma** and **Neochiropteris normalis**)
b	Row of sori between midrib and lamina margin more than 1 row…………………………………………………………....	**1. Neochiropteris**

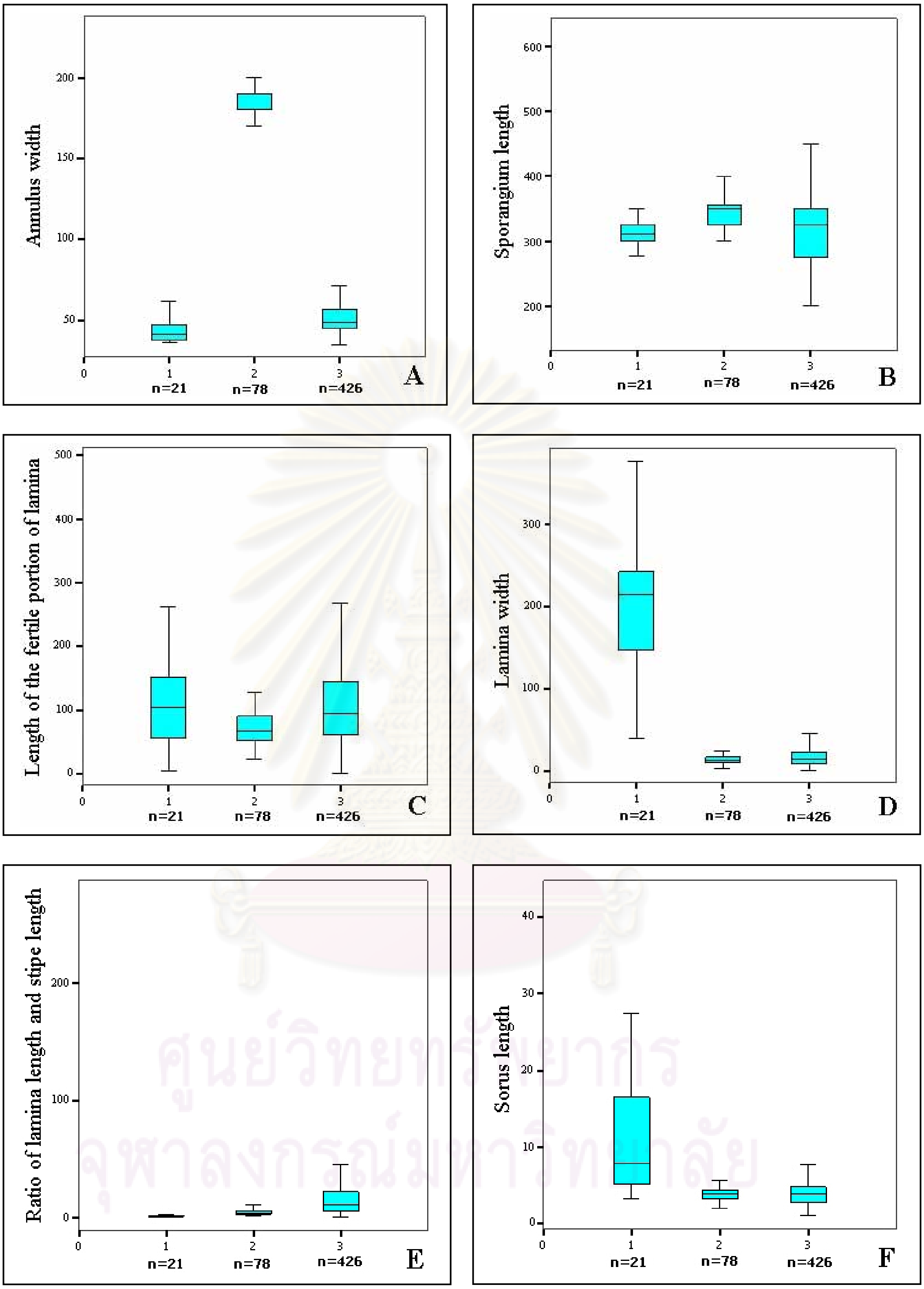

Figure 4.3 Box plots of the six important characters of the *Lepisorus* and related genera. A. annulus width, B. sporangium length, C. length of the fertile portion of lamina, D. lamina width, E. ratio of lamina length and stipe length, and F sorus length (1= the rest of *Neocheiropteri*s, 2= *Platygyria*, 3= *Lepisorus* (including *Paragramma* and *Neocheiropteris normalis* Tagawa)).

CHAPTER V

PHYLOGENETIC RELATIONSHIP

5.1 Introduction

Phylogenetics is a part of numerical taxonomy in the broad sense (Duncan and Baum, 1981). The phylogenetic approach was first introduced by German entomologist and systematic theorist Willi Hennig in a 1950 work entitled “Grundzuge einer Theorie der Phylogenetischen Systematik, and became widely known to English speakers in 1965 and 1966 under the name, “Phylogenetic systematics”. First labeled “Phylogenetic Systematics”, but now called “Cladistics”, this approach ,forcefully articulates the idea that genealogical relationships should be based on special similarity (shared derived characters or synapomorphies), and those relationships should be faithfully reflected in a formal hierarchic listing.

The phylogenetic approach is an important field for fern systematics. An improved phylogenetic framework of pteridophytes is required for developing classifications of land plants that reflect evolutionary history (Wolf, et al., 2000). As previous mentioned in Chapter II, it can be seen that these phylogenetic methods are valid and useful in solving classification problems in ferns.

In addition, as previously mentioned in Chapter II, the monophyletic genus *Lepisorus* is remains dubious and the circumscriptions of genus *Lepisorus were* conflicted by previous pteridologists who recognized to include or exclude two small genera, i.e. *Paragramma* or *Platygyria* in the genus *Lepisorus*.

5.1.1 Chapter aims

To clarify the delimitation of the *Lepisorus* and its small related taxa (*Paragramma*, *Platygyria* and *Neocheiropteris*) based on the phylogenetic analysis.

5.2 Materials and Methods

5.2.1 Plant materials

In the present study, the plant specimens from around the world kept in the herbaria in Europe (BM, E, L, K and P), in Asia (BCU, BKF, KUN and PYU) and personal collections from China and Thailand were studied. Most species were identified based on consulting type specimens and a few species were consulted specimens determined by pteridologists. In addition, identifications of these specimens were carried out by using identification keys from regional floras or taxonomic revisions, i.e. Ching (1933), Tagawa and Iwatsuki (1989), Zink (1993), Shieh et al. (1994), Hovenkamp (1998a, c), Verdcourt (2001), Lin, Y.-X. (2000) and Zhang, Liu and Xu (2003).

The ingroup taxa in the present study were *Lepisorus* sens.str. (recognized by Ching, 1933, 1940) and two small genera, i.e. *Paragramma* (recognized by Ching, 1940); Copeland, 1947; Pichi Sermolii, 1977) and *Platygyria* (recognized by Ching & S.K. Wu, 1980; Zhang et al, 2003*a*) and *Neocheiropteris* (recognized by Hennipman et al., 1990). In total, the ingroup taxa are thirty-eight species of the *Lepisorus*, 2 *Paragramma* species, 4 *Platygyria* species and 3 *Neocheiropteris* species).

In this study, genus *Pleopeltis* sens.str. (i.e. *the Pleopeltis* group of the *Polypodium* (Hennipman et al., 1990); Andrews and Windham, 1993; Verdcourt, 2001; Mickel and Smith, 2004) was excluded because it has been distinguished from *Lepisorus* sens.str. in terms of both morphology and anatomy. Their distinction was detailed by Zink (1988, 1993) and Rahaman and Sen (1999). Although some pteridologists, i.e. Copeland (1947) and Pichi Sermolii (1977) combined them, most recent taxonomic treatments e.g. Hennipman et al. (1990), Andrews and Windham (1993), Zink (1993), Hovenkamp (1998a, c), Verdcourt (2001), Mickel and Smith (2004) etc., have consented to keep them individually. Moreover, the recognition to maintain them as a separate taxa has been strongly supported by molecular systematic study (Schneider, 2004).

The total number of specimens were chosen to be studied comprised 579 specimens. (Appendix 2). *Belvisia mucronata* (Fée) Copel. and *Drymotaenium miyoshianum* Makino was chosen to be an ougroup because they are closely related to the present ingroup based on a broad exploration of the relationships of the polygrammoid ferns (Schneider et al. 2004).

5.2.2 Morphological and anatomical characters

The morphological and anatomical characters for the current study were studied and examined through personal evaluation and observation of the herbarium specimens. In all, thirty-three morphological and one anatomical characters (Table 5.1) were analyzed. These were coded in two different ways i.e. multistate or binary (presence/absence), and compiled to construct a data matrix (Appendix 3).

5.2.3 Data analysis

A phylogenetic analysis of the morphological anatomical dataset was performed with the program PAUP* 4.0b10 (Swofford, 1999) and the maximum parsimony method was conducted. All characters were treated as unordered and equally weighted. Heuristic search was then undertaken with stepwise random addition sequence, 100 random additional replications, MulTrees activated, Tree-Bisection-Reconnection (TBR) branch-swapping algorithm. As the data matrix was too large and required a lengthy period of time to complete the analysis, we set the Increase=auto, Maxtree=100, HSearch with NChuck=1000 and ChuckScore=1.

The robustness of each node was evaluated with the bootstrap procedure (1000 bootstrap replications; Felsenstein, 1985) using heuristic search (TBR branch-swapping, 5 random addition sequence per bootstrap replicate, MulTrees activated). To reduce time, NChuck=1000 and ChuckScore=1.

5.3 Results and Discussion

In the parsimony analysis of 33 morphological and anatomical characters, twenty-eight characters were parsimony-informative and the random additional sequence analysis found 181 most parsimonious trees (MPTs) in 1 island, with the following parameters: tree length 227 steps, consistency index (CI) excluding uninformative characters = 0.2556, homoplasy index (HI) excluding uninformative characters = 0.7444, retention index (RI) = 0.5688, rescaled consistency index (RC) = 0.1529.

The 50 percent majority rule consensus tree of 12 MPTs was shown in Figure 5.1. The tree topology mostly showed dichotomous resolution of the relationships and the percentage of trees in which the taxa or clades were together mostly were higher than 50 percent.

Using *Belvisia mucronata* (Fée) Copel. and *Drymotaenium miyoshianum* Makino as an outgroup, the result revealed that the ingroup was monophyletic, which supported with low bootstrap value (lower than 50%). The taxa of the ingroup clade shared acuminate lamina apex, sori at the position form the middle beween the midrib and lamina margin to close to midrib, sori mainly separate and sori mainly not oblique.

The ingroup was composed of 3 large clades (clades L1, L2 and L3) and *Lepisorus pseudonudus* Ching and *L. sublinearis* (Baker ex Takeda) Ching that formed a grade at base of the in group clade, but the relationships between Clades L1, L2 and L3 were unresolved. The taxa on clade L1 shared paltate rhizome scale, abaxial surface of lamina covered by few to moderate density of scales near the base, near or on midrib. The taxa of clade L2 shared entire margin of rhizome scales and rhizome scales clathrate at central region and the marginal region not clathrate. The taxa on clade L3 shared not glaucous rhizome surface, sori at the sori at the middle beween the midrib and lamina margin. Most clades within the ingroup clade were supported with low bootstrap support (lower than 50%). However, only a clade of *Lepisorus macrosphaerus* (Baker) Ching and *Neocheiropteris normalis* (D.Don) Tagawa was supported with 67% bootstrap value.

The result obtained from the present study may showed that the genus *Lepisorus* was paraphyletic (the ingroup clade) and this result was supported by one yielded by Schneider et al. (2004). The genus *Neocheiropteris* and *Paragramma* were polyphyletic (on clade L1, L2 and L3) while the genus *Platygyria* was monophyletic (on clade L3) while sharing the following characters states: (1) stomium position was not constant, (2) indurate cells were either absent, or few in number, (3) annulus widths more than 100 µm. However, the clades that were mentioned above were poorly supported by bootstrap analysis.

Table 5.1 List of thirty-three morphological and anatomical characters used in the phylogenetic analyses of the genus *Lepisorus* and its related genera.

Characters	States
1. rhizome surface	not glaucous (0), glaucous or not glaucous (1), glaucous (2).
2. presence of sclerenchyma strands in rhizome	absent (0), absent or present (1), present (2).
3. apex of rhizome scale	obtuse (0), obtuse or acute (1), acute or acuminate and not obtuse (2), filiform (3).
4. base of rhizome scale	obtuse or round (0), obtuse or round or cordate (1), cordate (2).
5. margin of rhizome scale	entire (0), entire or denticulate to dentate (1), denticulate to dentate (2).
6. shape of rhizome scale	lanceolate or triangular or ovate (0), circular mixed with lanceolate or triangular or ovate (1).
7. clathrate appearance of rhizome scale	clathrate_thoughout (0), clathrate thoughout or center clathrate with not clathrate margin (1), center clathrate with not clathrate margin (2), center clathrate with not clathrate margin or center opaque with clathrate or not clathrate margin (3), center opaque with clathrate or not clathrate margin (4).
8. orientation of rhizome scale	appress (0), appress or slightly spreading (1), slightly to strongly speading (2).
9. color of rhizome scale	one color (0), one or two colors (1), two colors (2).
10. attachment of rhizome scale	all scale basifixed (0), pseudopeltate or basifixed or peltate (1), all scale peltate (2).
11. appearance of hairs on upper surface of rhizome scale	glabrous (0), glabrous or hairy (1), hairy (2).
12. lobes of rhizome scale	absent (0), present and absent (1), present (2).
13. insertion point of rhizome scale	at base or close to base more than apex (0), at base or at the middle or close to base more than apex (1).
14. fertile and sterile frond appearance	monomorphic (0), hemidimorphic (1), hemidimorphic or dimorphic (2), dimorphic (3).

Table 5.1 (continued).

Characters	States
15. lamina indentation	margin entire or shallow waved or deep undulate (0), entire or pinnatifid or pinnatisect (1), 1-pinnate (2), basal part 1-pinnate and upper part pinnatisect (0), hastate or pedately dissected or palmately lobed (4).
16. lamina apex	acute (0), acute or acuminate (1), acute or acuminate or obtuse or round (2), acute or obtuse or round (3), acuminate (4), acuminate or obtuse or round (5), obtuse or round (6).
17. lamina base	attenuate_or cuneate (0), attenuate_or_cuneate_or_truncate (1), obtuse (2) truncate (3), cordate (4), hastate_or_sagitate (5).
18. lamina texture	membranaceous or chartaceous (0), membranaceous to coriaceous (1), subcoriaceous to coriaceous (2).
19. abaxial surface of lamina	glabrous (0), covered by few to moderate density of scales near the base, near or on midrib (1).
20. adaxial surface of lamina	glabrous (0), glabous or covered by few to moderate density of scales near the base, near or on midrib (1).
21. longitudinal posture of lamina margin	flat (0), slightly revolute (1), strongly revolute (2).
22. veins or lateral vein on abaxial surface of lamina	inconspicuous (0), present both inconspicuous and conspicuous (1), conspicuous (2).
23. symmetry of lamina base	symmetric or nearly symetric (0), present both symetric and asymetric base (1), distinctly asymmetric (2).
24. sori distribution between lamina base and apex	only on upper half (0), on upper half or reaching to the lower half (1), only on lower half (2).

Table 5.1 (continued).

Characters	States
25. sorus row number between midrib or rachis and the margin	one row (0), one or more than one row (1), more than one row (2).
26. sorus position between midrib (or rachis) and frond margin	only at the middle (0), at the middle to close to midrib (1), at the middle to close to the margin (2), close to midrib to close to the margin (3), only close to the midrib (4), only close to the margin (5)
27. sori type	mainly saparate (0), mainly coenosori (1).
28. sori paraphyses	not covered by clathrate paraphyses (0), covered by clathrate paraphyses (1).
29. sori orientation	not oblique (0), mainly not oblique and few oblique (1), dominant both oblique and not oblique (2), oblique (3).
30. stomium position	at the position between the epi and hypostomium (0), not constant position (1).
31. occurrence of indurate cells	many (0), absent or few (1)
32. annulus width	less than 90 µm (0), more than 100 µm.
33. large lateral vein at lamina base	absent (0), present (1)

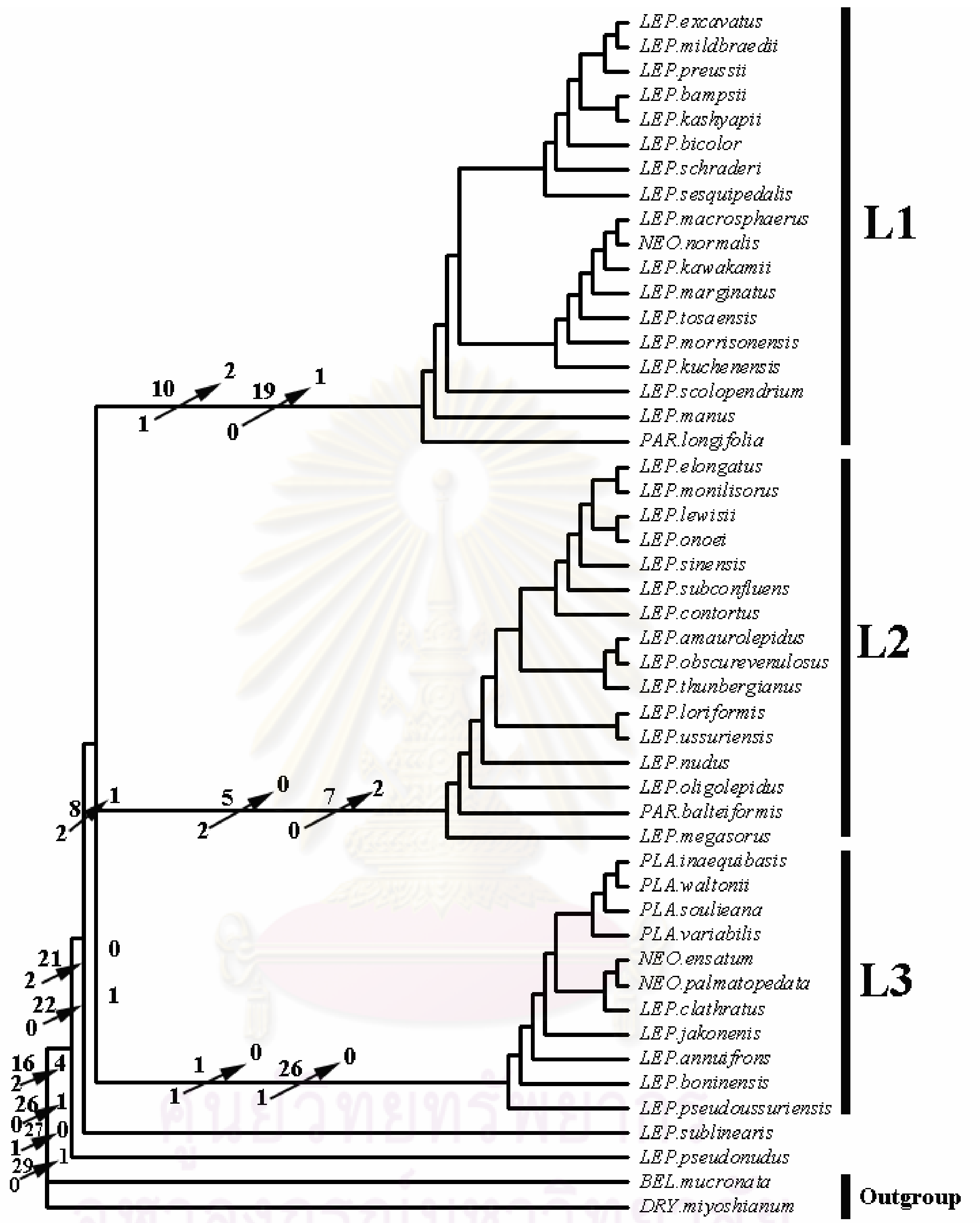

Figure 5.1 The 50 percent majority rule consensus tree of 12 MPTs and character state changes on some clades. Number above branch is a bootstrap value from 1000 replicates. Number above arrow=characters number, number at the start point of arrow= plesiomorhic state, number at the end of arrow head= derived state. LEP= *Lepisorus*, NEO= *Neocheiropteris*, PAR= *Paragramma*, PLA= *Platygyria*, L1-L3= indicate clades described in text.

5.4 Conclusion

The phylogenetic relationships of the genus *Lepisorus* and its related genera (i.e. *Paragramma Platygyria* and *Neocheiropteris* were analyzed based on 33 morphological and anatomical characters. However tree topology of the consensus tree mostly showed dichotomous branching, the statistics such as CI, RI, HI and RC determined that there were quite homoplasious in the entire data set on the trees. In addition, most clade on the consensus tree were poorly supported by the bootstrap analysis. Therefore, morphological and anatomical characters alone were of limited values in assessing relationships within genus *Lepisorus* and these related genera and phylognetic analysis based on these data cannot be used to clarify the generic circumscriptions of these taxa.

However, the phylogeny of these ferns is continues to require further analyses based on other data types such as molecular data or combining of morphological, anatomical and molecular data..

CHAPTER VI

GENERAL CONCLUSION

The fern genus *Lepisorus* (J. Smith) Ching s.l. or in the broad sense (including *Paragramma*) comprised of approximately 30 (Verdcourt, 2001) to 70 species (Lin, 2000) within the large family of Polypodiaceae. With members naturally occurring in tropical and subtropical Africa and tropical Asia extending northward to the Far East of Russia with one species in Hawaii, this is one of the most controversial fern genera in its taxonomic status. Based on similarities in appearance of morphological characters, *Lepisorus* and its related taxa, i.e. *Paragramma* and *Platygyria*, have sometimes been combined to form *Lepisorus* as a large genus. Holttum (1955), Tagawa and Iwatsuki (1989), Hennipman et al. (1990) and Hovenkamp, 1998a, c) recognized to merge the *Paragramma* with genus *Lepisorus* sens.str.. Yu and Lin, 1997b; Fraser-Jenkins, personal communication, 2008) recognized to merge the *Platygyria* with genus *Lepisorus* sens.str.. On the other hand, these taxa were regcognized by some pteridologists in a strict sense as separate genera as following: *Lepisorus* sens.str. recognized by Ching (1933, 1940); *Paragramma* recognized by Ching (1940), Copeland (1947) and Pichi Sermolli (1977); *Platygyria* was recognized by Ching and Wu (1980) and Zhang et al. (2003). In addition, the *Platygyria* was merged with genus *Neocheiropteris* (Hennipman et al., 1990).

The main aims of this thesis, therefore, was to clarify the circumscriptions of the genus *Lepisorus* and its related genera, i.e. *Paragramma* and *Platygyria*, which have been contradicted by previous pteridologists using phenetic and phylogenetic approaches.

In addition, the examinations of morphological and anatomical chatanters of genus *Lepisorus*, *Paragramma Platygyria*, and *Neocheiropteris* were also carried out.

The results based on phenetic approach can be proven to recognize that *Platygyria* was a distinct taxon from *Lepisorus* sens.str., *Paragramma* and *Neocheiropteris*. On the other hand, the circumscription of *Lepisorus* should include *Paragramma* and *Neocheiropteris normalis* Tagawa. Moreover, the rest of *Neocheiropteris* should be placed into a different group. Discriminant analyses revealed important quantitative characters that could be used for separating *Lepisorus* (including *Paragramma* and *Neocheiropteris normalis* Tagawa), *Platygyria* and the rest of *Neocheiropteris* by including annulus width, sporangium length, length of the fertile portion of lamina, lamina width, ratio of lamina length and stipe length, sorus length, ratio of stipe length and phyllopodia length, ratio of lamina length and lamina tip, spore length, number of sclerenchyma strand in rhizome, sporangium width and sorus width. Some of these characters, i.e. annulus width, and some useful qualitative characters, i.e occurrence of indurate cells, stomium position and row number of sori between midrib and lamina margin were used to construct a key to classify these ferns into 3 taxa as shown in Chapter 4. In addition, the results from examinations of morphology and anatomy support the result from phenetic analyses.

The result based on phylogenetic approach cannot be used to charify the circumscription of these ferns; however, tree topology of the consensus tree mostly showed dichotomous branching because the statistics such as CI, RI, HI and RC determined that there were quite homoplasious in the entire data set on the trees. In addition, most clade on the consensus tree were poorly supported by the bootstrap analysis.

In conclusion, the *Platygyria* should be treated as a distinct genus while the circumscription of the *Lepisorus* should be include *N. normalis* Tagawa and *Paragramma* and the rest of *Neocheiropteris* should be treated as a distinct genus based on the results obtained from phenetic analyzes.

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APPENDIX

Appendix 1. List of specimens examined for phenetic analyses.

Lepisorus amaurolepidus (Sledge) Bir & Trikha: Assgalston 1854 (Ceylon); Frances & Jarrett 629 (India); Fraser-Jenkins et al. 24 (Ceylon); Ghatak 84 (India); Jarrett 673 (India); Manickam 606 (India), 1180 (India), 34234 (India); Manickam & Matthew 34275 (India); Piggott 2673 (Ceylon); R.B. & Faden 1525 (Ceylon); Sledge 604A (Ceylon), 999 (Ceylon), 1025 (Ceylon), 1126 (Ceylon), 1182 (Ceylon), s.n. (Ceylon).

Lepisorus annuifrons (Makino) Ching: Faurie 5252 (Japan), s.n. (Japan); Fleet-Surgeon & Matthew s.n. 1 (Japan), s.n. 2 (Japan); Furuse 11349 (Japan); Kano et al. 26 (Japan); Makino s.n. (Japan); Seto 11864 (Japan); Suzuki 398002 (Japan); Tagawa 5813 (Japan); Tashiro 442 (Japan), s.n. (Japan).

Lepisorus bampsii (Pic. Serm.) M.J. Zink (= *Lepisorus excavatus* Ching): Bamp 2962 (Rwanda).

Lepisorus bicolor (Takeda) Ching: Chu 4127 (China); Duclaux 5044 (China); Henry 2465 (China), 10088 (China); Iwatsaki et al. 152 (China), 895 (China); Kato et al. 1419 (China); Kuan & Wang 2266 (China); Larsen, K. & S.S. Larsen 34416 (Thailand); Maxwell 94-1025 (Thailand), 95-1149 (Thailand); Rock 5887 (China); Schneider 2117 (China), 2956 (China); Smith 2088 (China), 12716 (China); Smitinand & Sleumer s.n. (Thailand); Smitinand et al. 7691 (Thailand); Steward et al. 649 (China); Tsai 59886 (China); Wilson 5317a (China); Winit 1201 (Thailand).

Lepisorus boninensis (Christ) Ching: Tuyama 512 (Japan); Warburg s.n. (Japan).

Lepisorus clathratus (C.B.Clarke) Ching: ACE 1214 (lowest specimen) (China); Chola Rangle 4300 (India); Cischison 183 (Afghanistan); Hope s.n.1 (India), s.n.2 (India); Ludlow et al. 17223 (Bhuthan); Wang 70755 (China).

Lepisorus contortus (Christ) Ching: Fleming 879 (Nepal); Giraldi s.n. (China); Hara et al. s.n. (India); Henry 6869 (China); Kato & Akiyama 2604 (China); Kato et al. 1725 (China); Kokonor-Tibet complex expedition 11693 (China), 11797 (China); Kuan & Wang 1922 (China); Ludlow et al. 15576 (China); Purdom 94 (China); Sherriff 7481 (India); Wilson 2633 (China); Zimmerman 396 (Nepal).

Lepisorus eilophyllus (Diels) Ching: Farges s.n. (China); Giraldi s.n. (China); Henry 6859 (China), s.n. (China); Purdom 90 (China); Rock 14719 (China); Soulié 23 (China); Wilson 2636 (China).

Lepisorus elongatus (Kaulf.) Ching: Gaudichaud s.n. (Sandwich Island); Hildebrand 18 (Hawaii).

Lepisorus excavatus (Bory ex Willd.) Ching: Alluaud 101 (Africa); Beals 154 (S. W. Jimma); Burger 505 (Ethiopia); De Witte 2274 (Congo Belge); Ghose 39 (China); Gilbert & Jeffort 4321 (Ethiopia); Hieronymus 8752 (Tanzania); Hooker & Thomson s.n. (China); Jacques-Felix 7154 (Africa); Kasner 2698 (Congo); Mindy 40 (Cameroon); Rehmann 5596 (Africa); Schelpe 5508 (Mozombique); Schimper 1560 (Ethiopia); Schlieben 3105 (Tanzania); Pichi Sermolli 6793 (Ethiopia); Uhlig 123 (Africa); Vincent 1186? (Réunion).

Lepisorus jakonensis (Blanf.) Ching (= *L. pseudonudus* Ching): Blanford 354 (India), s.n. (India).

Lepisorus mehrae Fraser-Jenk.: Datta 23475 (India); Steward 1494 (India).

Lepisorus kawakami (Hayata) Tagawa: Faurie s.n. (China); Tagawa 47 (China), 529 (China), 1854 (China), 2014 (China).

Lepisorus kuchenensis (Y.C. Wu) Ching: Cadiére 1126 (Indochina); Colani 2829 (Vietnam); Potelot 5213 (Vietnam); Poilane 17045 (Vietnam).

Lepisorus lewisii (Baker) Ching: Henry 9194B (China); Shearer s.n. (China); Tsang

23481 (China).

Lepisorus loriformis (Wall. ex Mett.) Ching: C.B.Clarke 12947 (India); Fleming 1734 (Nepal), 2086 (Nepal), 2089 (dup.1) (Nepal); Gamble 63834A (India); Gammie 319 (India); Hancock 92 (China); Henry 9194 (China), 11826 (China), 11826A (China), 13339 (China); Hooker s.n. (lelf specimen) (India); Hope s.n. (India); Keke 809 (Nepal); Rock 7303 (China); Wallich 271 (Nepal), 291 (Nepal).

Lepisorus macrosphaerus (Baker) Ching: Bodinier 1940 (China); Cadiere 1028 (Vietnam); Cavalerie 3748 (China), 7293 (China); Delavay 10 (China), 4358 (China); Duclaux 3352 (China); Faber 1063 (China); Hancock 49 (China); Henry 9203(1) (China), 9203(2) (China), 9203(3) (China), 13363 (China), 13633 (China); Kuan & Wang 1678 (China); Lecomte & Finet 528 (Indochina); Martin 1940 (China); Ombragie 36 (China); Omi 5321 (China); Poilane 26824 (Vietnam); Rock 6869 (China), 7538 (China); Tsai 51570 (China), s.n. (China).

Lepisorus manus Hovenkamp: De Wilde & De Wilde-Duyfjes 1305 (Indonesia), 15004 (Indonesia); Otto-Surbeck 365 (Indonesia); Surbeck 644 (Indonesia).

Lepisorus marginatus Ching: Zhang 1 (China).

Lepisorus megasorus (C.Chr.) Ching: Hancock 31 (China); Poilane 5113 (Indochina).

Lepisorus mildbraedii (Hieron.) Pic.Serm. (= *L. excavatus* Ching): Le Walle 1284 (Burundi), 2442 (Burundi); Taton 270 (Congo-Belge).

Lepisorus monilisorus (Hayata) Tagawa: Chang 4400 (Taiwan); Faurie 475 (China), 594 (China).

Lepisorus morisonensis (Hayata) H.Ito: Tagawa 417 (China).

Lepisorus nudus (Hook.) Ching: Ballard 1035 (Ceylon), 1107 (Ceylon), 1199

(Ceylon); Beddome s.n. (India); Dharmsani 2028 (Nepal); Fraser-Jenkins et al. 53 (Ceylon), 104 (Ceylon), 200 (Ceylon); Gamble 12507 (India), 17451 (India), 27437 (India); Hancock 13 (China); Hara et al. s.n. (Nepal); Henry 13129 (China); Jarrett 544 (India), 565 (India); Mesz 2500 (India); Minickam 600 (India); Mooney 2809 (India), 4174 (India); Panigrahi 5071 (India); Perrottet 652 (India); Piggott 2676 (Ceylon); Saldanha & Ramamoorthy 528 (India); Saldanha 14568 (India); Stewart 21047 (India); Tagawa 417 (China); Thomson s.n. 1 (lower-right specimen) (India), s.n. 2 (India), s.n. 3 (India); Thwites 1295 (Ceylon); Walker T196 (Ceylon); Wenger 72 (India).

Lepisorus obscure-venulosus (Hayata) Ching: Faurie 472 (China); Ito s.n. (Japan); Liao 927 (Taiwan); Poilane 25575 (Indochina), 25577 (Indochina); Shimizu & Chuang 20418 (Taiwan); Wang et al. 604 (Taiwan); Yao 8636 (China).

Lepisorus oligolepidus (Baker) Ching: Cavalerie 34 (China), 1579 (China), 3748 (China); Henry 2049 (China), 9062 (China), 10192 (China); Macre 1926 (China); Matthew 31 (China), s.n. 1 (China), s.n. 2 (China), s.n. 3 (China); Sivestri 3443 (China).

Lepisorus onoei (Franch. & Sav.) Ching: Asakura s.n. (Japan); Faurie 2867 (Japan); Furuse 10430 (Japan), 10626 (Japan); Iwatsuki 1540 (Japan); Iwatsuki et al. 5566 (Japan), 6504 (Japan); Matthew 167 (Japan), s.n. 1 (Japan), s.n. 2 (Japan); Meries s.n. (Japan); Ohba 662598 (Japan); Oyama 15531 (Japan); Savatier s.n. (Japan); Taquet 3993 (Korea), 3995 (Korea), 3999 (Korea); Togashi 1215 (Japan), s.n. (Japan); Umemura s.n. (Japan); Watanbe s.n. (Japan).

Lepisorus preussii (Hieron.) Pic.Serm.: Brunt 764 (Cameroon); Chapman 62 (Nigeria); Daramola, 41577 (Cameroon); Letouzey 8908 (Cameroon); Morton 2582 (Sierra Leone); Saxer 13 (Cameroon).

Lepisorus pseudonudus Ching: Luo 237(64) (China); Wilson 2633 (China).

Lepisorus pseudo-ussuriensis Tagawa: Faurie 591(China), 644 (China); Tagawa s.n. (China).

Lepisorus schraderi (Mett.) Ching: Bigger 2009 (Tanzania); Chase 6568 (Rhodesia), 42276 (Rhodesia); Hutchinson & Gillett 4286 (Rhodesia); Loveridge 392 (Uganda); Osmaston 3717 (Uganda), 3879 (Uganda); Pichi Sermolli, P. 5141 (Tanzania).

Lepisorus scolopendrium (Ching) Mehra & Bir: Anderson 1486 (India); Beddome s.n. (India); Blanford s.n. (India); Bunchuai 219 (Thailand), 1493 (Thailand); Drummond 23381 (India); Gamble 8212 (India), 10237 (India), s.n. (India); Hancock 104 (China), K39 (China); Hennipman 3151a (Thailand); Henry 10087 (China), 13070A (China); Hooker s.n. 1 (India), s.n. 2 (India); Hope s.n. (India); Iwatsuki et al. 9404 (Thailand), 9585 (Thailand), 11095 (Thailand); Keke, 234A (Nepal), 234B (Nepal), 261 (Nepal), 1078 (Nepal); Kerr 1980 (Thailand), 6328 (Thailand); Maxwell 02-220 (Thailand); Murata et al. 15720 (Thailand), 15962 (Thailand), 15963 (Thailand); Rock 6677 (China); Shimizu et al. 11441 (Thailand), 18568 (Thailand), 18884 (Thailand); Smith 1184 (Thailand); Smitinand et al. 1744 (Thailand); SP.19 31907 (Thailand); Tagawa et al. 1510 (Thailand), 1512 (Thailand), 9310 (Thailand); Thomson s.n. (India); Winit 1175 (Thailand).

Lepisorus sesquispedalis (J.Sm.) Fraser-Jenkins (= *L. scolopendrium* (Ching) Mehra & Bir): Chola Rangle 4399 (India); Duthie 5183 (India); Hooker & Thomson s.n. (India); Kari 176 (China); Suguwlawbbeel 397 (India).

Lepisorus subconfluens Ching: Hennipman 3141 (Thailand), 3375 (Thailand);

Iwatsuki et al. 9589 (Thailand), 11096 (Thailand); Murata et al. 15050 (Thailand); Rock 8727 (China); Snitinand 4667 (Thailand); Smitinand & Sleumer 8306 (Thailand); Tsai 57888 (China), 59879 (China); Winit 1152 (Thailand).

Lepisorus sublinearis (Baker ex Takeda) Ching: Hancock 83 (China); Henry 9062A (China), 11827 (China), 13603 (China); Tagawa et al. 2878 (Thailand).

Lepisorus thunbergianus (Kaulf.) Ching: Bowring s.n. (China); Cheo s.n. (China); Cox et al. 198 (China), 1093 (China); CW 566 (China); Delavay s.n. (China); Dorsett & Dorsett 3048 (China); Fan & Li 434 (China), s.n. (China); Fang s.n. (China); Furuse 1849 (Japan), 4757 (Japan), 9884 (Japan); Ghose 8 (China); Hancock 30 (China), 73 (Japan), 111 (China); Harland s.n. (China); Hutoh 17011 (Japan); Merrill s.n. (China); Perdom 93 (China); Taquet 3656 (Korea); Wilson 53179 (China); Yao 10462 (China).

Lepisorus tosaensis (Makino) H.Ito: Tagawa & Iwasuki 3716 (Japan).

Lepisorus ussuriensis (Regel & Maack) Ching: Furuse 7138 (Japan), 7186 (Japan), 9162 (Japan); Komrov 46 (China); Litwinow s.n. (Manduhuria oriental); Matthew s.n. (Japan); Maxinowig s.n. (Japan); Mizushima 10264, (Japan); Savatier 1541 (Japan); Tagawa 764 (Japan); Tashiro 443 (Japan); Tsiang 7625 (China).

Neocheiropteris palmatopedata Christ: Beauvais 830 (China); Chang 808 (China); Feng 145 (China), 633 (China), 2542 (China); Kokonor Tibet complex expedition 13339 (China); Qin 83 (China); Qiu 60746 (China); Liou 147 (China), 4729 (China), 13884 (China); Wu 770 (China), 100918 (China); Xin 83 (China).

Paragramma longifolia (Blume) T. Moore: Abdullah 71 (Malesia); Boonkerd 1191

(Thailand); Borssum 1943 (Indonesia); Cadière 791 (Vietnam); Charoenphol et al. 3962 (Thailand); Edano 35625 (Philippines); Edwards 195 (Malesia); Henderson 24832 (Singapore); Holttum 20794 (Singapore); Hope s.n. (Burma); Iwatsuki et al. T14512 (Thailand); Kerr 14137 (Thailand), 14492 (Thailand); Laman et al. TL868 (Indonesia); Lee UL-48 (Malesia); Matthew s.n. (Malesia); Mjoberg s.n. (Indinesia); Moysey 33663 (Malesia); Parris 6984 (Indonesia); Poilane 19451 (Indochina), 19468 (Indonesia); Ramos 20397 (Philippines), 30196 (Philippines), 33336 (Philippines); Sinclair 10610 (Malesia); Smith 2015 (Thailand); Smitinand 934 (Thailand), 2774 (Thailand); Weber 1150 (Philippines).

Platygyria inaequibasis Ching & S.K. Wu: Fang & Dong 1839 (China); Li & Wang 20658 (China); Wang 66249 (China), 70118 (China); Wu et al. 75-771 (China), 5953 (China); Zhang (Dian team) 1753 (China).

Platygyria soulieana (Christ) X.C. Zhang & Q.R. Liu: Delavay 207/1 (China), 207/2 (China), 207/3 (China), 6893 (China); Li 3 (China), 8 (China), 10 (China).

Platygyria variabilis Ching & S.K. Wu: Ching 23475 (China), 23960 (China); Chu 310 (China), 797 (China), 851 (China), 874 (China), 1459 (China), 17557 (China), 23560 (China); Chu & Feng, 747 (China), 766 (China), 797 (China), 828 (China), 874 (China), 933 (China), 944 (China), 1459 (China), s.n. 1 (China), s.n. 2 (China); Chu et al. 747 (China), 17540 (China), 17557 (China), 29029 (China); Chu & Yan 24448 (China); Dongchuan team 63-139 (China); Duttuc 432 (India); Evans et al. 86-299 (China), 8663 (China); Fang 1838 (China); Feng 2882 (China), 8969 (China); Kato et al. 1154 (China), 1670 (China), 1673 (China); Meili Team 26498 (China); Northeast Yunnan team 63-6678 (China), 230 (China); Pan s.n. (China); Sykes & Williams 3503 (Nepal);

Team 32 (China), s.n. (China); Wang 68344 (China), 69556 (China), 69900 (China); Wraber 345 (Nepal); Wu et al. 4953 (China); Yu 11692 (China), 12303 (China), 12393 (China), 14010 (China), 7133 (China), 8996 (China); Zhang & Guo 2371 (China).

Platygyria waltonii (Ching) Ching & S.K. Wu: Littledale s.n. (China); Tibetean team 74-3626 (China); Waddell s.n. (China); Walton s.n. 1 (China); Walton s.n. 2 (China); Walton s.n. 3 (China); Zhang 1551 (China).

Appendix 2. List of specimens examined for morphological and anatomical studies and phylogenetic analysis.

Belvisia mucronata (Fée) Copel.: Croft & Lelean 65774 (New Guinea); Cuming 92 (Philippines); Edwards 2119 (Malaysia); Elmer 6967 (Philippines), 14214 (Philippines); Gardner 1303 (Ceylon); Jauvol 560 (Caledonia); Parris & Croxall 9404 (New Guinea); Womersley & Van Roger 5892 (New Guinea).

Drymotaenium miyoshianum Makino: Delavay s.n. (China); George Forest 13593 (China), 20116 (China), 23568 (China), 28914 (China); Henry 9149 (China); Kingdon-Ward 910 (China), 19261 (China); Luo Yi-Bo 86 (China); Rock 10057 (China); Schneider 1073 (China); Soulie 867 (China), s.n. (China); Tagawa (duplicate 1)2032 (China), s.n. (China), s.n. (China); Tsai 59929 (China), 63106 (China); Tsiang 9192 (China); Umemura s.n.1 (Japan), s.n.2 (Japan), s.n.3 (Japan); Wilson 2638 (China); Wu 4623 (China), 4060 (China).

Lepisorus amaurolepidus (Sledge) Bir & Trikha: Assgalston 1854 (Ceylon); Frances & Jarrett 629 (India); Fraser-Jenkins et al. 24 (Ceylon); Ghatak 84 (India); Jarrett 673 (India); Manickam 606 (India), 1180 (India), 34234 (India); Manickam & Matthew 34275 (India); Piggott 2673 (Ceylon); R.B. & Faden 1525 (Ceylon); Sledge 604A (Ceylon), 999 (Ceylon), 1025 (Ceylon), 1126 (Ceylon), 1182 (Ceylon), s.n. (Ceylon).

Lepisorus annuifrons (Makino) Ching: Faurie 5252 (Japan), s.n. (Japan); Fleet-Surgeon & Matthew s.n. 1 (Japan), s.n. 2 (Japan); Furuse 11349 (Japan); Kano et al. 26 (Japan); Makino s.n. (Japan); Seto 11864 (Japan); Suzuki 398002 (Japan); Tagawa 5813 (Japan); Tashiro 442 (Japan), s.n. (Japan).

Lepisorus bampsii (Pic. Serm.) M.J. Zink (= *Lepisorus excavatus* Ching): Bamp 2962 (Rwanda).

Lepisorus bicolor (Takeda) Ching: Chatan W. 406 (Thailand), 407 (Thailand), 408 (Thailand), 470 (Thailand); Chu 4127 (China); Duclaux 5044 (China); Henry 2465 (China), 10088 (China); Iwatsuki et al. 152 (China), 895 (China); Kato et al. 1419 (China); Kuan & Wang 2266 (China); Larsen, K. & S.S. Larsen 34416 (Thailand); Maxwell 94-1025 (Thailand), 95-1149 (Thailand); Rock 5887 (China); Schneider 2117 (China), 2956 (China); Smith 2088 (China), 12716 (China); Smitinand & Sleumer s.n. (Thailand); Smitinand et al. 7691

(Thailand); Steward et al. 649 (China); Tsai 59886 (China); Wilson 5317a (China); Winit 1201 (Thailand).

Lepisorus boninensis (Christ) Ching: Tuyama 512 (Japan); Warburg s.n. (Japan).

Lepisorus clathratus (C.B.Clarke) Ching: ACE 1214 (lowest specimen) (China); Chola Rangle 4300 (India); Cischison 183 (Afghanistan); Hope s.n.1 (India), s.n.2 (India); Ludlow et al. 17223 (Bhuthan); Wang 70755 (China).

Lepisorus contortus (Christ) Ching: Fleming 879 (Nepal); Giraldi s.n. (China); Hara et al. s.n. (India); Henry 6869 (China); Kato & Akiyama 2604 (China); Kato et al. 1725 (China); Kokonor-Tibet complex expedition 11693 (China), 11797 (China); Kuan & Wang 1922 (China); Ludlow et al. 15576 (China); Purdom 94 (China); Sherriff 7481 (India); Wilson 2633 (China); Zimmerman 396 (Nepal).

Lepisorus eilophyllus (Diels) Ching: Farges s.n. (China); Giraldi s.n. (China); Henry 6859 (China), s.n. (China); Purdom 90 (China); Rock 14719 (China); Soulié 23 (China); Wilson 2636 (China).

Lepisorus elongatus (Kaulf.) Ching: Gaudichaud s.n. (Sandwich Island); Hildebrand 18 (Hawaii).

Lepisorus excavatus (Bory ex Willd.) Ching: Alluaud 101 (Africa); Beals 154 (S. W. Jimma); Burger 505 (Ethiopia); De Witte 2274 (Congo Belge); Ghose 39 (China); Gilbert & Jeffort 4321 (Ethiopia); Hieronymus 8752 (Tanzania); Hooker & Thomson s.n. (China); Jacques-Felix 7154 (Africa); Kasner 2698 (Congo); Mindy 40 (Cameroon); Rehmann 5596 (Africa); Schelpe 5508 (Mozombique); Schimper 1560 (Ethiopia); Schlieben 3105 (Tanzania); Pichi Sermolli 6793 (Ethiopia); Uhlig 123 (Africa); Vincent 1186? (Réunion).

Lepisorus jakonensis (Blanf.) Ching (= *L. pseudonudus* Ching): Blanford 354 (India), s.n. (India).

Lepisorus mehrae Fraser-Jenk.: Datta 23475 (India); Steward 1494 (India).

Lepisorus kawakami (Hayata) Tagawa: Faurie s.n. (China); Tagawa 47 (China), 529 (China), 1854 (China), 2014 (China).

Lepisorus kuchenensis (Y.C. Wu) Ching: Cadiére 1126 (Indochina); Colani 2829 (Vietnam); Potelot 5213 (Vietnam); Poilane 17045 (Vietnam).

Lepisorus lewisii (Baker) Ching: Henry 9194B (China); Shearer s.n. (China); Tsang 23481 (China).

Lepisorus loriformis (Wall. ex Mett.) Ching: C.B.Clarke 12947 (India); Fleming 1734

(Nepal), 2086 (Nepal), 2089 (dup.1) (Nepal); Gamble 63834A (India); Gammie 319 (India); Hancock 92 (China); Henry 9194 (China), 11826 (China), 11826A (China), 13339 (China); Hooker s.n. (lelf specimen) (India); Hope s.n. (India); Keke 809 (Nepal); Rock 7303 (China); Wallich 271 (Nepal), 291 (Nepal).

Lepisorus macrosphaerus (Baker) Ching: Bodinier 1940 (China); Cadiere 1028 (Vietnam); Cavalerie 3748 (China), 7293 (China); Delavay 10 (China), 4358 (China); Duclaux 3352 (China); Faber 1063 (China); Hancock 49 (China); Henry 9203(1) (China), 9203(2) (China), 9203(3) (China), 13363 (China), 13633 (China); Kuan & Wang 1678 (China); Lecomte & Finet 528 (Indochina); Martin 1940 (China); Ombragie 36 (China); Omi 5321 (China); Poilane 26824 (Vietnam); Rock 6869 (China), 7538 (China); Tsai 51570 (China), s.n. (China).

Lepisorus manus Hovenkamp: De Wilde & De Wilde-Duyfjes 1305 (Indonesia), 15004 (Indonesia); Otto-Surbeck 365 (Indonesia); Surbeck 644 (Indonesia).

Lepisorus marginatus Ching: Zhang 1 (China).

Lepisorus megasorus (C.Chr.) Ching: Hancock 31 (China); Poilane 5113 (Indochina).

Lepisorus mildbraedii (Hieron.) Pic.Serm. (= *L. excavatus* Ching): Le Walle 1284 (Burundi), 2442 (Burundi); Taton 270 (Congo-Belge).

Lepisorus monilisorus (Hayata) Tagawa: Chang 4400 (Taiwan); Faurie 475 (China), 594 (China).

Lepisorus morisonensis (Hayata) H.Ito: Tagawa 417 (China).

Lepisorus nudus (Hook.) Ching: Ballard 1035 (Ceylon), 1107 (Ceylon), 1199 (Ceylon); Beddome s.n. (India); Chatan W. 411 (Thailand), 412 (Thailand), 413 (Thailand), 414 (Thailand), 415 (Thailand), 421 (Thailand), 423 (Thailand), 424 (Thailand), 426 (Thailand), 427 (Thailand), 430 (Thailand), 464 (Thailand), 465 (Thailand), 466 (Thailand), 467 (Thailand), 469 (Thailand), 470 (Thailand), 471 (Thailand), 473 (Thailand); Dharmsani 2028 (Nepal); Fraser-Jenkins et al. 53 (Ceylon), 104 (Ceylon), 200 (Ceylon); Gamble 12507 (India), 17451 (India), 27437 (India); Hancock 13 (China); Hara et al. s.n. (Nepal); Henry 13129 (China); Jarrett 544 (India), 565 (India); Mesz 2500 (India); Minickam 600 (India); Mooney 2809 (India), 4174 (India); Panigrahi 5071 (India); Perrottet 652 (India); Piggott 2676 (Ceylon); Saldanha & Ramamoorthy 528 (India); Saldanha 14568 (India); Stewart 21047 (India); Tagawa 417 (China); Thomson s.n. 1 (lower-right specimen) (India), s.n. 2

(India), s.n. 3 (India); Thwites 1295 (Ceylon); Walker T196 (Ceylon); Wenger 72 (India).

Lepisorus obscure-venulosus (Hayata) Ching: Faurie 472 (China); Ito s.n. (Japan); Liao 927 (Taiwan); Poilane 25575 (Indochina), 25577 (Indochina); Shimizu & Chuang 20418 (Taiwan); Wang et al. 604 (Taiwan); Yao 8636 (China).

Lepisorus oligolepidus (Baker) Ching: Cavalerie 34 (China), 1579 (China), 3748 (China); Henry 2049 (China), 9062 (China), 10192 (China); Macre 1926 (China); Matthew 31 (China), s.n. 1 (China), s.n. 2 (China), s.n. 3 (China); Sivestri 3443 (China).

Lepisorus onoei (Franch. & Sav.) Ching: Asakura s.n. (Japan); Faurie 2867 (Japan); Furuse 10430 (Japan), 10626 (Japan); Iwatsuki 1540 (Japan); Iwatsuki et al. 5566 (Japan), 6504 (Japan); Matthew 167 (Japan), s.n. 1 (Japan), s.n. 2 (Japan); Meries s.n. (Japan); Ohba 662598 (Japan); Oyama 15531 (Japan); Savatier s.n. (Japan); Taquet 3993 (Korea), 3995 (Korea), 3999 (Korea); Togashi 1215 (Japan), s.n. (Japan); Umemura s.n. (Japan); Watanbe s.n. (Japan).

Lepisorus preussii (Hieron.) Pic.Serm.: Brunt 764 (Cameroon); Chapman 62 (Nigeria); Daramola, 41577 (Cameroon); Letouzey 8908 (Cameroon); Morton 2582 (Sierra Leone); Saxer 13 (Cameroon).

Lepisorus pseudonudus Ching: Luo 237(64) (China); Wilson 2633 (China).

Lepisorus pseudo-ussuriensis Tagawa: Faurie 591(China), 644 (China); Tagawa s.n. (China).

Lepisorus schraderi (Mett.) Ching: Bigger 2009 (Tanzania); Chase 6568 (Rhodesia), 42276 (Rhodesia); Hutchinson & Gillett 4286 (Rhodesia); Loveridge 392 (Uganda); Osmaston 3717 (Uganda), 3879 (Uganda); Pichi Sermolli, P. 5141 (Tanzania).

Lepisorus scolopendrium (Ching) Mehra & Bir: Anderson 1486 (India); Beddome s.n. (India); Blanford s.n. (India); Bunchuai 219 (Thailand), 1493 (Thailand); Chatan W. 401 (Thailand), 402 (Thailand), 403 (Thailand), 404 (Thailand), 409 (Thailand), 410 (Thailand), 453 (Thailand), 454 (Thailand), 460(Thailand); Drummond 23381 (India); Gamble 8212 (India), 10237 (India), s.n. (India); Hancock 104 (China), K39 (China); Hennipman 3151a (Thailand); Henry 10087 (China), 13070A (China); Hooker s.n. 1 (India), s.n. 2 (India); Hope s.n. (India); Iwatsuki et al. 9404 (Thailand), 9585 (Thailand), 11095 (Thailand); Keke, 234A (Nepal), 234B (Nepal), 261 (Nepal), 1078 (Nepal); Kerr 1980

(Thailand), 6328 (Thailand); Maxwell 02-220 (Thailand); Murata et al. 15720 (Thailand), 15962 (Thailand), 15963 (Thailand); Rock 6677 (China); Shimizu et al. 11441 (Thailand), 18568 (Thailand), 18884 (Thailand); Smith 1184 (Thailand); Smitinand et al. 1744 (Thailand); SP.19 31907 (Thailand); Tagawa et al. 1510 (Thailand), 1512 (Thailand), 9310 (Thailand); Thomson s.n. (India); Winit 1175 (Thailand).

Lepisorus sesquispedalis (J.Sm.) Fraser-Jenkins (= *L. scolopendrium* (Ching) Mehra & Bir): Chola Rangle 4399 (India); Duthie 5183 (India); Hooker & Thomson s.n. (India); Kari 176 (China); Suguwlawbbeel 397 (India).

Lepisorus sinensis (Christ) Ching: Henry 10434/1 (China), 10434/2 (China), 10434/3 (China), 13072 (China); Hancock 196 (China); Iwatsuki, K. et al. s.n. (Thailand); Tagawa, M. et al. 9973 (Thailand); Iwatsuki, K. et al. 9586 (Thailand).

Lepisorus subconfluens Ching: Chatan W. 428 (Thailand), 429 (Thailand); Hennipman 3141 (Thailand), 3375 (Thailand); Iwatsuki et al. 9589 (Thailand), 11096 (Thailand); Murata et al. 15050 (Thailand); Rock 8727 (China); Snitinand 4667 (Thailand); Smitinand & Sleumer 8306 (Thailand); Tsai 57888 (China), 59879 (China); Winit 1152 (Thailand).

Lepisorus sublinearis (Baker ex Takeda) Ching: Chatan W. 405 (Thailand); Hancock 83 (China); Henry 9062A (China), 11827 (China), 13603 (China); Tagawa et al. 2878 (Thailand).

Lepisorus thunbergianus (Kaulf.) Ching: Bowring s.n. (China); Cheo s.n. (China); Cox et al. 198 (China), 1093 (China); CW 566 (China); Delavay s.n. (China); Dorsett & Dorsett 3048 (China); Fan & Li 434 (China), s.n. (China); Fang s.n. (China); Furuse 1849 (Japan), 4757 (Japan), 9884 (Japan); Ghose 8 (China); Hancock 30 (China), 73 (Japan), 111 (China); Harland s.n. (China); Hutoh 17011 (Japan); Merrill s.n. (China); Perdom 93 (China); Taquet 3656 (Korea); Wilson 53179 (China); Yao 10462 (China).

Lepisorus tosaensis (Makino) H.Ito: Tagawa & Iwasuki 3716 (Japan).

Lepisorus ussuriensis (Regel & Maack) Ching: Furuse 7138 (Japan), 7186 (Japan), 9162 (Japan); Komrov 46 (China); Litwinow s.n. (Manduhuria oriental); Matthew s.n. (Japan); Maxinowig s.n. (Japan); Mizushima 10264, (Japan); Savatier 1541 (Japan); Tagawa 764 (Japan); Tashiro 443 (Japan); Tsiang 7625 (China).

Neocheiropteris ensata Ching (Ching, 1933) (=*Microsorum ensatum* (Thunb.) H.Ito (Nooteboom, 1997): Boufford et al. 24070 (China); Cavalerie 33 (China); Gustav Mann. s.n. (India); Oldham s.n. (Japan); Tagawa & Iwasuki 539 (Japan); Togasi 427 (Japan).

Neocheiropteris normalis (D.Don) Ching: Beusekom and Phengklai 2473 (Thailand); Beusekom and Smitinand 2196 (Thailand), 2214 (Thailand); Hennipman 3393 (Thailand); Iwatsuki and Fukuoka T7196 (Thailand); Konta, Phengklai and Khao-Iam 4934 (Thailand); Larsen et al. 34421(Thailand); Maxwell 97-136 (Thailand); Murata et al. T15645 (Thailand); T15958 (Thailand); Phengklai et al. 7020 (Thailand), 7131 (Thailand); Phengklai, Konta and Khao-Iam 11421 (Thailand); Shimizu et al. T11599 (Thailand), T20537 (Thailand); Smitinand 5516 (Thailand); Tagawa, Iwatsuki and Fukuoka T1503 (Thailand), T2457 (Thailand), T2885 (Thailand); Wongprasert sn. (Thailand).

Neocheiropteris palmatopedata Christ (Ching, 1933) (=*Microsorum* palmatopedata (Baker) Noot. (Nooteboom, 1997): Beauvais 830 (China); Chang 808 (China); Ching 24814 (China); Feng 145 (China), 633 (China), 2542 (China); Huarg 775 (China); Kokonor Tibet complex expedition 13339 (China); Li 15 (China); Liou 147 (China), 4729 (China), 13884 (China); Qin 83 (China); Qiu 54403 (China); Qiu 60746 (China); Wu 153 (China); 770 (China), 100918 (China); Xin 83 (China).

Paragramma balteiformis (Brause) Hovenkamp: Brass 12075(Papua New Guinea), 23289 (Papua New Guinea).

Paragramma longifolia (Blume) T. Moore: Abdullah 71 (Malesia); Boonkerd 1191 (Thailand); Borssum 1943 (Indonesia); Cadière 791 (Vietnam); Charoenphol et al. 3962 (Thailand); Edano 35625 (Philippines); Edwards 195 (Malesia); Henderson 24832 (Singapore); Holttum 20794 (Singapore); Hope s.n. (Burma); Iwatsuki et al. T14512 (Thailand); Kerr 14137 (Thailand), 14492 (Thailand); Laman et al. TL868 (Indonesia); Lee UL-48 (Malesia); Matthew s.n. (Malesia); Mjoberg s.n. (Indinesia); Moysey 33663 (Malesia); Parris 6984 (Indonesia); Poilane 19451 (Indochina), 19468 (Indonesia); Ramos 20397 (Philippines), 30196 (Philippines), 33336 (Philippines); Sinclair 10610 (Malesia); Smith 2015 (Thailand); Smitinand 934 (Thailand), 2774 (Thailand); Weber 1150 (Philippines).

Platygyria inaequibasis Ching & S.K. Wu: Fang & Dong 1839 (China); Li & Wang

20658 (China); Wang 66249 (China), 70118 (China); Wu et al. 75-771 (China), 5953 (China); Zhang (Dian team) 1753 (China).

Platygyria soulieana (Christ) X.C. Zhang & Q.R. Liu: Delavay 207/1 (China), 207/2 (China), 207/3 (China), 6893 (China); Li 3 (China), 8 (China), 10 (China).

Platygyria variabilis Ching & S.K. Wu: Ching 23475 (China), 23960 (China); Chu 310 (China), 797 (China), 851 (China), 874 (China), 1459 (China), 17557 (China), 23560 (China); Chu & Feng, 747 (China), 766 (China), 797 (China), 828 (China), 874 (China), 933 (China), 944 (China), 1459 (China), s.n. 1 (China), s.n. 2 (China); Chu et al. 747 (China), 17540 (China), 17557 (China), 29029 (China); Chu & Yan 24448 (China); Dongchuan team 63-139 (China); Duttuc 432 (India); Evans et al. 86-299 (China), 8663 (China); Fang 1838 (China); Feng 2882 (China), 8969 (China); Kato et al. 1154 (China), 1670 (China), 1673 (China); Meili Team 26498 (China); Northeast Yunnan team 63-6678 (China), 230 (China); Pan s.n. (China); Sykes & Williams 3503 (Nepal); Team 32 (China), s.n. (China); Wang 68344 (China), 69556 (China), 69900 (China); Wraber 345 (Nepal); Wu et al. 4953 (China); Yu 11692 (China), 12303 (China), 12393 (China), 14010 (China), 7133 (China), 8996 (China); Zhang & Guo 2371 (China).

Platygyria waltonii (Ching) Ching & S.K. Wu: Littledale s.n. (China); Tibetean team 74-3626 (China); Waddell s.n. (China); Walton s.n. 1 (China); Walton s.n. 2 (China); Walton s.n. 3 (China); Zhang 1551 (China).

Appendix 3. Data matrix of morphological and anatomical character states for each species studied. (BEL= *Belvisia*, DRY= *Drymotaenium*, LEP= *Lepisorus*, PAR= *Paragramma*, PLA= *Platygyria*, NEO= *Neocheiropteris*).

Taxon/Characters	111111111122222222223333 123456789012345678901234567890123
BEL *mucronata* (Fée) Copel.	022020022100010501002100??1100000
DRY miyoshianum Makino	012020022100000202002001?01100000
LEP *annuifrons* (Makino) Ching	022120112201000100000210000110000
LEP *amaurolepidus* (Sledge) Bir & Trikha	022020420202000201101111030110000
LEP *bampsii* (Pic. Serm.) M.J. Zink	222021220200000600100201040130000
LEP *bicolor* (Takeda) Ching	122020300202000400110211010110000
LEP *boninensis* (Christ) Ching	022020012102000002000010000110000
LEP *clathratus* (C.B.Clarke) Ching	012020022100000400100211000110000
LEP *contortus* (Christ) Ching	012020420202000102102001030110000
LEP *eilophyllus* (Diels) Ching	022220022100000002002000000100000
LEP *elongatus* (Kaulf.) Ching	012020410102000102001000000100000
LEP *excavatus* (Bory ex Willd.) Ching	112010012202000500111211030110000
LEP *jakonenis* (Blanf.) Ching	022020012100000000000201000110000
LEP *kawakamii* (Hayata) Tagawa	122001200220000102101000020110000
LEP *kuchenensis* (Y.C. Wu) Ching	010000200200000400000211010130000
LEP *lewisii* (Baker) Ching	022020420202000002002000010100000
LEP *loriformis* (Wall. ex Mett.) Ching	022020022100000101101001030110000
LEP *macrosphaerus* (Baker) Ching	0200012002200000011012110501100000
LEP *mehrae* Fraser-Jenk.	222020210202000400110201040130000
LEP *manus* Hovenkamp	122000212100000400000011040110000
LEP *marginatus* Ching	022001200222000000100001000130000
LEP *megasorus* (C.Chr.) Ching	022021012200000302100101010110000
LEP *mildbraedii* (Hieron.) Pic.Serm.	022020210202000500111201010110000
LEP *monilisorus* (Hayata) Tagawa	021021210122000002001010000100000
LEP *morrisonensis* (Hayata) H.Ito	022000220200000400000201040110000
LEP *nudus* Ching	022000212200000101101101030110000
LEP *obscure-venulosus* (Hayata) Ching	022000420102000001101110000110000
LEP *oligolepidus* (Baker) Ching	022020410200000401111111040110000
LEP *onoei* (Franch. & Sav.) Ching	022000410200000602002000000110000
LEP *preussii* (Hieron.) Pic.Serm	122020210100000400111201010110000
LEP *pseudonudus* Ching	022020022100000402002001010130000
LEP *pseudo-ussuriensis* Tagawa	022020012100000001000000010110000
LEP *schraderi* (Mett.) Ching	222020202202000200100211010110000
LEP *scolopendrium* (Ching) Mehra & Bir	122000200100000201100111010110000
LEP *sesquipedalis* (J.Sm.) Fraser-Jenk.	122010200202000600000210010110000
LEP *sinensis* (Christ) Ching	022020410200000001101001?21100000
LEP *subconfluens* Ching	022020420202000101111001000100000

Appendix 3. (continued.)

Taxon/Characters	1111111111222222222233333 123456789012345678901234567890123
LEP *thunbergianus* (Kaulf.) Ching	022020320202000201101101030110000
LEP *tosaensis* (Makino) H.Ito	022020400200000400000000010110000
LEP *ussuriensis* (Regel & Maack) Ching	122021422100000101111011030110000
PAR *balteiformis* (Brause) Hovenkemp	002020012100000612101201040110000
PAR *longifolia* (Blume) T. Moore	122020002100000202001111050110000
PLA *inaequibasis* Ching & S.K. Wu	023020040100001300100211010111110
PLA *soulieana* (Christ) X.C. Zhang & Q.R. Liu	122120002100000600000211040111110
PLA *variabilis* Ching & S.K. Wu	012021022100000600000001000111110
PLA *waltonii* (Ching) Ching & S.K. Wu	022020022120004600100211130111110

BIOGRAPHY

Mr.Wannachai Chatan was born on March 30, 1972 in Mahasarakham Province. He was graduated in Biology from Khonkean University in 1996. In 2000, he received his Master of Science in Botany from Department of Botany, Faculty of Science, Chulalongkorn University. Then in 2003, he pursued his study in Biological Science Ph.D. Program, Faculty of Science, Chulalongkorn University.