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PHENETIC RELATIONSHIP BETWEEN *LEPISORUS* (J.SM.) CHING (PTERIDOPHYTA: POLYPODIACEAE) AND ITS RELATED GENERA

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Abstract

Multivariate analyses based on morphological and anatomical characters have been performed to investigate the phenetic relationship and to clarify the circumscriptions of the genus *Lepisorus* (J.Sm.) Ching and its related genera, namely *Neocheiropteris* Christ, *Paragramma* T. Moore and *Platygyria* Ching & S.K. Wu. The dendrogram of cluster analysis separated the plants into three groups at Gower similarity coefficient 0.75. Group 1 and Group 2 consisted of *Neocheiropteris palmatopedata* (Baker) H. Christ and four species of *Platygyria*, respectively. Group 3 was *Neocheiropteris ensata* Ching and two species of *Paragramma* deeply embedded in the *Lepisorus s.s.* Canonical discriminant analysis supported the classification inferred from the clustering results. Based on these results, *Platygyria* and *N. palmatopedata* should be recognized as distinct genera. On the other hand, *N. ensata* and the genus *Paragramma* should be merged to the genus *Lepisorus*.

Introduction

Lepisorus (J.Sm.) Ching *s.l.* (including *Paragramma* T. Moore) is the fern genus of Polypodiaceae, which comprised approximately 30 species (Verdcourt, 2001) 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). *Lepisorus s.s.* (excluding the *Paragramma*), however, was first treated by J. Smith in 1846 (in Zink, 1993) as a section of a highly heterogeneous *Drynaria*, and Ching (1933) raised the section *Lepisorus* to generic rank. The common features of *Lepisorus s.l.* are epiphytic, epilithic or terrestrial ferns with short- to long-creeping rhizome covered by clathrate scales; laminas are simple, entire and mostly naked; and sori are borne in single rows on either side of the midrib, and covered by clathrate paraphyses (Hennipman *et al.*, 1990; Verdcourt, 2001).

Until now, the generic circumscription of *Lepisorus* has remained controversial because it sometimes included or excluded its related taxa, namely *Paragramma* and *Platygyria* Ching & S.K. Wu. In addition, *Platygyria*, which is closely related to *Lepisorus s.l.* sometimes merged with the genus *Neocheiropteris* Christ.

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The genus *Paragramma* was founded by T. Moore in 1857 using *P. longifolia* T. Moore as the type species (Copeland, 1947). Until now, its separation from the *Lepisorus s.l.* has never been clear (Hovenkamp, 1998). The recognition to keep it as a distinct genus was followed by Ching (1940), Copeland (1947) and Pichi Sermolli (1977). Copeland (1947) used the combination characters of soral shape and the presence of lamina scales to distinguish the *Paragramma* from *Pleopeltis* (including *Lepisorus s.s.*). Two species, namely *Paragramma balteiformis* Copeland and the type species, were recognized by Copeland (1947). In contrast, Holttum (1954), Tagawa and Iwatsuki (1989), Hennipman *et al.* (1990) and Hovenkamp (1998) consented to unite *Paragramma* with *Lepisorus s.s.*

The Chinese fern genus *Platygyria* was erected based on the *P. waltonii* (Ching) Ching & S.K. Wu (Ching and Wu, 1980) and the characters of sporangium were used as the important defining characters. So, five species, namely *Platygyria sinuata* Ching & S.K. Wu, *P. inaequibasis* Ching & S.K. Wu, *P. variabilis* Ching & S.K. Wu, *P. kongtingensis* Ching & Y.X. Lin and *P. muliensis* Ching & S.K. Wu were recognized (Ching and Wu, 1980; Ching *et al.*, 1983). Likewise, Zhang *et al.* (2003) agreed to keep *Platygyria* at the genus level and treated *P. kongtingensis* and *P. muliensis* as two synonyms of *P. variabilis*. However, there were other two treatments of the genus *Platygyria*. The first involved reducing *Platygyria* under *Neocheiropteris* (Ching, 1933; Hennipman *et al.*, 1990), while the second involved merging *Platygyria* with *Lepisorus s.s.* (Yu and Lin, 1997). Therefore, the merging of *Platygyria* with either *Lepisorus* or *Neocheiropteris*, or its acceptance as a distinct genus needs to be assessed.

As the controversial generic circumscription or position of these taxa shown above, until now, there has been no taxonomic study aimed at clarifying these problems. Therefore, the objectives of the present work were, 1) to investigate the phenetic relationship and use the result to determine the suitability of the generic circumscription or position of the *Lepisorus* and the other three related genera, i.e. *Neocheiropteris*, *Paragramma* and *Platygyria*, and 2) to determine the important morphological or anatomical characters that can be used to distinguish these taxa. With the aforesaid objectives in mind, both cluster analysis (CA) and discriminant analysis (DA) were performed based on 53 qualitative and quantitative characters examining 487 herbarium specimens.

Materials and Methods

Plant materials: In the present study, about 2500 herbarium specimens collected from around the world and housed at the herbaria in Europe (BM, E, L, K and P) and Asia (BCU, BKF, BK, PE, KUN, PYU and TI) were studied (Herbarium abbreviations according to Holmgrens and Holmgrens, 2008). A total of 487 complete specimens were selected for examination constituting the Operational Taxonomic Units (OTUs). (Some representative specimens are listed in Appendix I. A complete list is available upon request from the corresponding author.) The specimens that were included in this study belonged to *Lepisorus s.s.* and its related three genera, namely *Neocheiropteris*, *Paragramma* and *Platygyria*. These specimens included specimens of the type species of each genus. Most specimens were identified by examining type specimens or identifications were made by consulting literature, e.g. Ching (1933), Tagawa and Iwatsuki (1989), Zink (1993), Shieh *et al*. (1994), Hovenkamp (1998), Verdcourt (2001), and Zhang *et al.* (2003).

Morphological and anatomical characters: Fifty-three morphological and anatomical characters were examined for each of the 487 specimens. Measurement was carried out by using a Keiba digital caliper No. 111-101HB or specimens were measured under Stereomicroscope (Zeiss Stemi DV4) and light microscopes (Olympus CH30). Of these characters, 26 were quantitative including four ratio characters (Appendix II), and 27 were qualitative characters scored as binary or multi-state characters (Appendix III). These characters and their states were used to construct a data matrix.

Phenetic analysis: The phenetic relationships among the taxa were investigated by two types of multivariate analysis: cluster analysis (CA) and canonical discriminant analysis (DA). The CA was performed by using an unweighted pair-group method with arithmetic average (UPGMA) clustering implemented in the Multivariate Statistical Package (MVSP), Version 3.13 (Kovack Computing Services) to place individual specimen into groups. Because the characters submitted to analysis were both quantitative and qualitative, the Gower similarity coefficient (GSC) was calculated (Gower, 1971) and clustered by the group-average method of the MVSP program.

A subset of characters that maximized differences among the groups determined by CA or other groups (i.e. *Lepisorus s.s.*, *Paragramma*, *Platygyria* and *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. The canonical discriminant analyses was performed by using the CLASSIFY procedure in SPSS/PC for Windows, release 10.0 (Anonymous, 1999).

Results and Discussion

Cluster Analysis (CA): The UPGMA dendrogram that constructed using GSC measure showed three discrete groups (Fig. 1) at GSC 0.75. Group 1 included *Neocheiropteris palmatopedata* and Group 2 comprised the four species of *Platygyria*. In addition, Group 3 was the largest group consisting of *Lepisorus s.s.*, *N. ensata* and the two species of *Paragramma*.

At Gower similarity coefficient 0.71, these fern taxa were divided into two groups, i.e. Group 1 and a group composed of Groups 2 and 3 (Fig. 1). Group 1 is distinct from the rest mainly by the combination characters of pedatifid lamina, presence of large veins at the lamina base and lamina width (more than 120 mm) as shown in the key to the genera below. The result suggested that *N. palmatopedata* was far distinct from the rests while the genus *Platygyria* was more closely related to the genus *Lepisorus* and *Paragramma* than *N. palmatopedata*. In addition, genus *Lepisorus*, *N. ensata* and *Paragramma* are closely related to each other than the rest.

Canonical Discriminant Analysis (DA): DA was divided into two analyses based on the number of prior groups obtained: 1) four groups, including *Lepisorus s.s.*, *Neocheiropteris*, *Paragramma* and *Platygyria*, all of which were assigned based on previous recognized genera (such as Christ, 1905; Ching, 1940; Copeland, 1947; Pichi Sermolli, 1977; Ching and Wu, 1980; Zhang *et al.*, 2003); and 2) three groups, including Groups 1, 2 and 3, which were obtained from CA. Overall, 26 quantitative characters were used in these analyses with a purpose to test their groupings.

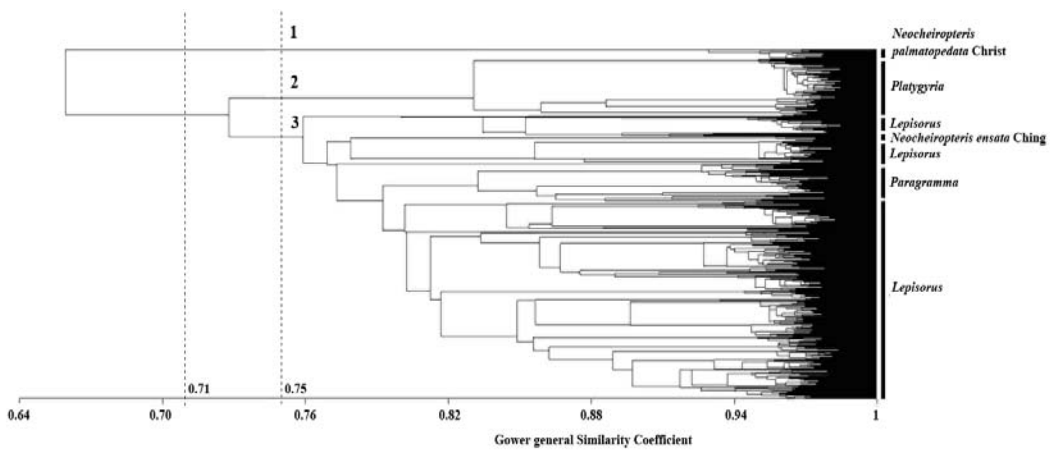

Fig. 1. UPGMA clustering of 487 Operational Taxonomic Units (OTUs) based on 53 quantitative and qualitative characters of *Lepisorus*, *Paragramma*, *Platygyria* and *Neocheiropteris*.

Once the stepwise analysis had been performed for all four groups, the linear discriminant function classification showed that 97.3% of the specimens had been correctly classified. The nature of the differences between the entries were shown by the pooled within canonical structure wherein canonical variable 1 was 97.3% correlated with the 26 quantitative characters and explained 86.2% of the total variance, which was highly associated with three characters (Table 1). Canonical variable 2 was 81.6% correlated with the quantitative characters and explained 9.7% of the total variance, which was highly associated with four characters. Canonical variable 3 was 68.1% correlated with the quantitative characters and explained 4.2% of the total variance, which was highly associated with seven characters (Table 1).

Table 1. 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 (Appendix II) scored in this study. Characters in bold were selected by stepwise discriminant analysis for further use in canonical discriminant analysis. *indicates the large absolute correlation between each variable and any discriminal functions.

Characters	Discriminant function		
	1	2	3
AW	.954*	-.018	.007
NM	-.079*	.058	-.032
SPOL	.055*	-.012	-.038
LL	-.049	.017	.034
LW	-.003	.520*	-.126
SL	-.014	.440*	.086
STL	.056	.364	.014
LLST	.087	.359*	-.007
PHD	-.086	.337*	.256
STPH	-.081	-.264	.201
RHDM	-.048	.232	.063
RSWI	-.061	.222	-.005
STD	-.097	.201	.195
RSLE	.034	.129	-.100
SPW	.041	-.054	.041
NSSR	-.091	-.055	.464*
PHL	-.045	.181	.390*
LLLF	.027	.075	.250*
RHLI	-.081	.135	-.218*
LFPL	-.026	.024	.210*
SW	-.010	-.036	-.192*
LLLT	.003	.129	-.178
LASL	-.031	.148	-.164
RHSI	-.020	.071	-.136
SPOW	.108	-.057	.133*
SPL	.045	.000	.049

The stepwise analysis was carried out for the three groups, i.e. these groups were split by the UPGMA dendrogram using GSC at 0.75. The nature of the differences between the entries was shown by the pooled within the canonical structure wherein canonical variable 1 was 97.2% correlated with the 26 quantitative characters and explained 89.7% of the total variance, which was highly associated with three characters (Table 2). Canonical variable 2 was 81.6% correlated with the quantitative characters and explained 10.3% of the total variance which was highly associated with seven characters (Table 2). The linear discriminant function classification (Table 3) obtaining from the program showed that the specimens had been 100% correctly classified; obviously, therefore, this

Table 2. Pooled within canonical structure of three groups (i.e. *Lepisorus* (including *Paragramma*), *Platygyria* and *Neocheiropteris*) obtained from CA based on 26 quantitative characters (Appendix II). Characters in bold were selected by stepwise discriminant analysis for further use in canonical discriminant analysis. * indicates the large absolute correlation between each variable and any discriminal functions.

Characters	Discriminant function 1	Discriminant function 2	Characters	Discriminant function 1	Discriminant function 2
AW	.968*	-.033	STPH	-.069	-.258
LLLF	.085	.082	PHD	-.008	.235
LL	-.070	.012	STD	-.072	.219
SPOW	.069	.022	RHDM	-.014	.205
SPOL	.056*	.013	RSWI	-.042	.159
NM	-.034	.019	**NSSR**	-.088	-.147*
LFPL	-.027*	-.023	RHLI	.013	.145
LW	-.002	.503*	SPW	.032	-.126
SL	-.014	.453*	SPL	.040	-.119
LASL	-.030	.333	RSLE	.059	.099
LLLT	.018	.310*	RHSI	.017	.093
LLST	.087	.310*	**PHL**	-.043	.092*
STL	.043	.306	**SW**	-.010	.033*

Table 3. Classification Function Coefficients of three groups (i.e. *Lepisorus* (including *Paragramma*), *Platygyria* and *Neocheiropteris*) obtained from CA based on the 26 quantitative characters (Appendix II). This linear discriminant function classification received from the program showed that the specimens had been 100% correctly classified.

Characters	Categories		
	Lepisorus (including *Paragramma*)	*Platygyria*	*Neocheiropteris*
NSSR	-0.201	-0.099	-0.026
PHL	-9.480	-6.281	-6.687
LW	13.926	3.554	4.198
SL	25.130	2.926	3.254
SW	-8.708	-3.013	-2.182
LFPL	2.936	7.615	7.031
SPOL	0.116	0.134	0.100
AW	0.302	1.306	0.365
LLST	0.119	0.290	-1.834
LLLT	1.230	-0.967	-1.146
(Constant)	-89.828	-163.867	-49.985

function could be used for further identification of these ferns. To identify an unknown specimen, one needs to multiply each character score by its coefficient in each column, compute the total for each column, the column with the highest total is the group to which the specimen belongs.

The ordination plot on the two canonical axes obtained from the four groups analysis (Fig. 2) showed that canonical axis 1 divided these plants into two main groups, one group included *Lepisorus s.s.*, *Paragramma* and *Neocheiropteris*, and the other consisting solely of *Platygyria*. However, canonical axis 2 was able to separate *N. palmatopedata* from the rest. Therefore, these two axes could divide these ferns into three groups. Furthermore, these results were similar when the plants were divided into three groups based on the result of CA (not shown).

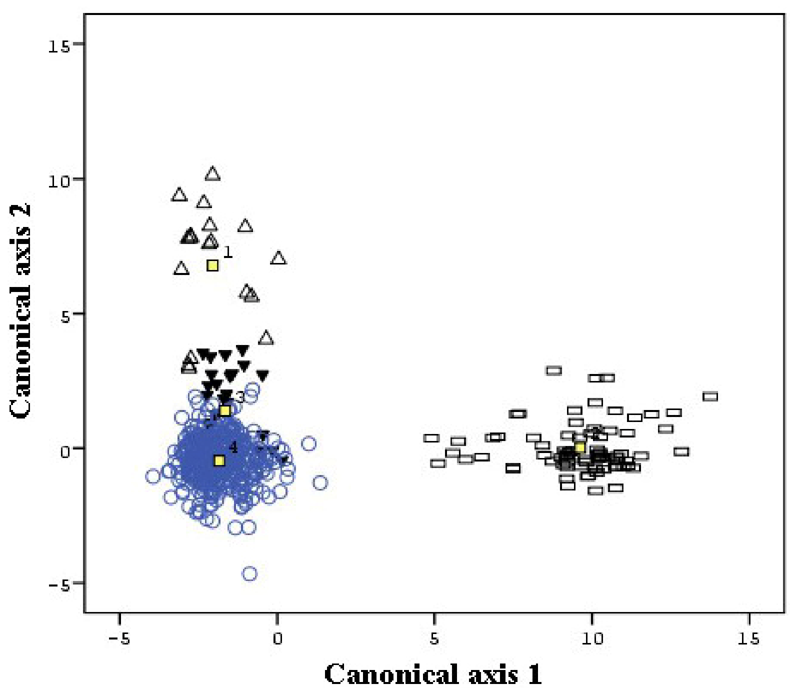

Fig. 2. Ordination plot on the canonical axes 1 and 2 of the four priori assigned groups (O: *Lepisorus*, ▼: *Paragramma*, □: *Platygyria*, Δ: *Neocheiropteris*).

Circumscription of **Lepisorus** *and* **Paragramma**

As far as the taxonomic position or circumscription of the *Paragramma* is concerned, there are two different forms of recognition so far, i) the form that maintains them as a distinct genus (Ching, 1940; Copeland, 1947; Pichi Sermolli, 1977) and ii) the form that combines the *Paragramma* with *Lepisorus s.s.* (Holttum, 1954; Tagawa and Iwatsuki, 1989; Hennipman *et al.*, 1990; Hovenkamp, 1998). The key characters that Copeland

(1947) used to distinguish *Paragramma* from his *Pleopeltis* (i.e. including *Lepisorus s.s.*) were the combination of its soral shape and the presence of lamina scales. In Copeland's key to genera of Polypodiaceae, as well as 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* generally had round or elongate sori or fused sori, but the elongate-sori species had peltate scales on the lamina.

It was observed from this study that *Paragramma longifolia* and *P. balteiformis* had round sori together with elongate sori. *Paragramma longifolia*, however, had glabrous lamina while few clathrate scales occurred on the lamina of *P. balteiformis*. Moreover, both elongate sori and few scales on the lower surface of lamina could have occurred in some *Lepisorus* species, for example *L. angustus* Ching, *L. subconfluens* Ching and *L. scolopendrium* Tagawa. So, the combination of lamina scales and soral shape could not be used to separate *Paragramma* from *Pleopeltis*. Accordingly, *Paragramma* could not also be separated from *Lepisorus* by using these characters.

The results of both CA and DA strongly indicated that *Paragramma* and *Neocheiropteris ensata* were not distinct from *Lepisorus s.s.*, so the genus *Paragramma* should be treated as a synonym of the genus *Lepisorus*. Likewise, *N. ensata* should be treated as a species of the genus *Lepisorus*. Furthermore, Fraser-Jenkins (1997) noted that *N. ensata* is a misapplied name of *N. ovata* (Fée) Fras.-Jenk. Bosman *et al.* (1998), however, recognized *N. ensata* as *Microsorum ensatum* (Thunb.) H. Itô, but also noted that their justification was based on a single specimen from Malesia. They also added that *M. ensatum* is probably a hybrid between a species of *Lepisorus* and a true *Microsorum* species.

The results from this study, therefore, strongly support the recognition of Tagawa and Iwatsuki (1989), Hennipman *et al.* (1990) and Hovenkamp (1998) that the circumscription of the genus *Lepisorus* must include *Paragramma*. In addition, the new finding is that *N. ensata* should be transferred to the genus *Lepisorus*.

Circumscription of **Neocheiropteris** *and* **Platygyria**

For *Platygyria*, three taxonomic positions have been recognized, i.e. combining with *Lepisorus s.s.* (Yu and Lin, 1997; C.R. Fraser-Jenkins, personal communication), treating it under *Neocheiropteris* (Ching, 1933; Hennipman *et al.*, 1990) and maintaining the status of distinct genus (Ching and Wu, 1980; Zhang *et al.*, 2003). Firstly, the *Platygyria* was proposed as a genus of *Polypodiaceae* by Ching and Wu in 1980 wherein the characters used to define this taxon were the globose sporangium and the very broad annulus consisting of scarcely indurate cell walls. Fraser-Jenkins (1997) had an opinion that *P. variabilis* should belong to *Lepisorus clathratus* (C.B. Clarke) Ching and the rest of *Platygyia* appeared to belong to *Phymatopteris* Pic. Serm. because according to him the type-species, *Platygyia waltonii*, is in fact a *Phymatopteris*, another genus of the

Polypodiaceae. However, the genus *Phymatopteris* is not recognized by Hennipman *et al.* (1990) and Smith *et al*. (2006). It was suggested that annulus characters are not constant (C.R. Fraser-Jenkins, personal communication), while Zhang *et al.* (2003) determined that they are rather stable. After studying *Platygyria* in comparison with *Lepisorus*, *Neocheiropteris* and *Paragramma*, it was found that the annulus characters were not only important in separating *Platygyria* from *Neocheiropteris*, but also from *Lepisorus* and *Paragramma*. However, when herbarium specimens were examined, we found that some specimens having both sporangia which were globose, having very broad annulus (≥ 105 μm) and few indurate cells of annulus (i.e. indurate cells of annulus 1-5 or less than 1/5 of annulus or absent) and sporangia which were flat or slightly flat, having narrow annulus (<100 μm) and prominent indurate cells (i.e. more than half of annulus are indurate cell). It was found from this study that these specimens were mixed with specimens of *Lepisorus clathratus* and were placed in the folder of *Lepisorus clathratus* complex. However, they should be separated from *L. clathratus* and put into the genus *Platygyria*.

In addition, the position of the stomium is an important character to distinguish the *Platygyria* from the rest. 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. Most ferns had a row of indurate cells for the annulus, and this row were also interrupted by thin wall cells of epistomium, stomium and hypostomium. The stomium in most ferns could occur between the epi- and hypostomium, but it could not occur on the row of indurate cells of annulus. In *Platygyria*, however, 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* could not be of constant occurrence as in other ferns and can be present throughout or slightly throughout the annulus.

The tuft of hairs dorsally attached to the rhizome scales has been given much weight by Ching (1933) and Tagawa and Iwatsuki (1989) as a characteristic of their *Neocheiropteris s.l.* Examinations of this characteristic found that these hairs could also be found in *Neocheiropteris palmatopedata*, *N. ensata* and *Platygyria waltonii*, but they were not found in the other *Platygyria* species. 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 characteristic could not be considered as a diagnostic characteristic of *Neocheiropteris*.

Moreover, according to both CA and DA, *Platygyria*, *Lepisorus s.l.* and *Neocheiropteris* were split into three distinct groups (Figs 1 and 2). These results were supported by the recognition of Ching and Wu (1980) and Zhang *et al.* (2003) in maintaining *Platygyria* as a distinct taxon. Therefore, the characteristics of the *Platygyria* were globose sporangia, very broad annulus (≥ 105 μm) and few indurate cells of annulus (i.e. indurate cell of annulus 1-5 or less than 1/5 of annulus or absent). In addition, the circumscription of *Platygyria* should include the species or specimens that have similar characters.

Neocheiropteris palmatopedata, the type species and one of the two representatives of the genus *Neocheiropteris* in this study should be kept under *Neocheiropteris*. The striking characters that have never been used as key characters to distinguish it and the other taxa are pedatifid laminas and the presence of large veins at the lamina base. Also, the lamina width is between 147-376 mm while less than 100 mm lamina width found in the rest taxa. Thus the result is also supported by CA and DA.

Previously, *Lepisorus s.s.* (Ching, 1933, 1940), *Paragramma* (Ching, 1940; Copeland, 1947; Pichi Sermolli, 1977) and *Platygyria* (Ching and Wu, 1980; Zhang *et al.*, 2003) were recognized as separate genera by some pteridologists. Also, *Neocheiropteris* was recognized as a distinct genus from the genera above (Christ, 1905). The results were examined in terms of morphology and anatomy, and the two multivariate analyses of which can be proven to recognize that *Platygyria* was a distinct taxon from *Lepisorus*, *Neocheiropteris* and *Paragramma*. Moreover, *N. palmatopedata* should be put into a different group. On the other hand, the circumscription of *Lepisorus* should include *N. ensata* and *Paragramma*.

This study found ten important quantitative characters that could be used for splitting *Lepisorus* (including *N. ensata* and *Paragramma*), *N. palmatopedata* (here it is recognized as a monotypic genus) and *Platygyria* by including the annulus width, sporangium length, length of the fertile portion of lamina, lamina width, sorus length, ratio of lamina length and lamina tip length, ratio of lamina length and stipe length, number of sclerenchyma strand in rhizome, phyllopodia length, and sorus width. Some of these characters, including annulus width and lamina width, and some useful qualitative characters i.e. lamina indentation, prominent large vein at lamina base, occurrence of indurate cells and stomium position were used to construct a key to genera as below:

Key to genera

1a.	Annulus width ≥ 105 µm, indurate cell of annulus 1-5 or absent, stomium not constantly positioned on annulus (rarely not as above)	**Platygyria**
1b.	Annulus width ≤ 95 µm, indurate cell are more than half of annulus cells, stomium between the thin wall epi- and hypostomium	**2**
2a.	Lamina pedatifid, lamina width ≥ 120 mm, large vein at lamina base present	**Neocheiropteris**
2b.	Lamina margin entire or undulate, lamina width < 120 mm, large vein at lamina base absent	**Lepisorus** (including *Neocheiropteris ensata* and *Paragramma*)

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Appendix I. **A list of representative specimens of each species examined.**

-Lepisorus amaurolepidus (Sledge) Bir & Trikha: Fraser-Jenkins et al. 24 (Ceylon); Jarrett 673 (India); Manickam 606 (India). ***-L. annuifrons*** (Makino) Ching: Faurie 5252 (Japan); Kano et al. 26 (Japan); Makino s.n. (Japan). ***-L. bampsii*** (Pic. Serm.) M.J. Zink (= ***L. excavatus*** Ching): Bamp 2962 (Rwanda). ***-L. bicolor*** (Takeda) Ching: Duclaux 5044 (China); Henry 2465 (China); Maxwell 94-1025 (Thailand). ***-L. boninensis*** **(Christ) Ching**: Tuyama 512 (Japan); Warburg s.n. (Japan). ***-L. clathratus*** (C.B. Clarke) Ching: Chola Rangle 4300 (India); Cischison183 (Afghanistan); Ludlow et al. 17223 (Bhuthan). ***-L. contortus*** (Christ) Ching: Fleming 879 (Nepal); Henry 6869 (China); Zimmerman 396 (Nepal). ***-L. eilophyllus*** (Diels) Ching: Henry 6859 (China); Purdom 90 (China); Wilson 2636 (China). ***-L. elongatus*** (Kaulf.) Ching: Gaudichaud s.n. (Sandwich Island); Hildebrand 18 (Hawaii). ***-L. excavatus*** (Bory ex Willd.) Ching: Burger 505 (Ethiopia); Ghose 39 (China); Pichi Sermolli 6793 (Ethiopia). ***-L. jakonensis*** (Blanf.) Ching (= ***L. pseudonudus*** Ching): Blanford 354 (India), s.n. (India). ***-L. mehrae*** Fraser-Jenk.: Datta 23475 (India); Steward 1494 (India). ***-L. kawakami*** (Hayata) Tagawa: Faurie s.n. (China); Tagawa 47 (China). ***-L. kuchenensis*** (Y.C. Wu) Ching: Cadiére 1126 (Indochina); Colani 2829 (Vietnam); Poilane 17045 (Vietnam). ***-L. lewisii*** (Baker) Ching: Henry 9194B (China); Shearer s.n. (China); Tsang 23481 (China). ***-L. loriformis*** (Wall. ex Mett.) Ching: C.B.Clarke 12947 (India); Fleming 1734 (Nepal), Wallich 271 (Nepal). ***-L. macrosphaerus*** (Baker) Ching: Cavalerie 3748 (China); Duclaux 3352 (China); Poilane 26824 (Vietnam). -

L. manus Hovenkamp: De Wilde & De Wilde-Duyfjes 1305 (Indonesia); Otto-Surbeck 365 (Indonesia); Surbeck 644 (Indonesia). -***L. marginatus*** Ching: Zhang 1 (China). -***L. megasorus*** (C.Chr.) Ching: Hancock 31 (China); Poilane 5113 (Indochina). -***L. mildbraedii*** (Hieron.) Pic.Serm. (= ***L. excavatus*** Ching): Le Walle 1284 (Burundi), 2442 (Burundi); Taton 270 (Congo-Belge). -***L. monilisorus*** (Hayata) Tagawa: Chang 4400 (Taiwan); Faurie 475 (China), 594 (China). -***L. morisonensis*** (Hayata) H.Ito: Tagawa 417 (China). -***L. nudus*** (Hook.) Ching: Ballard 1035 (Ceylon); Dharmsani 2028 (Nepal); Stewart 21047 (India). -***L. obscure-venulosus*** (Hayata) Ching: Faurie 472 (China); Poilane 25575 (Indochina); Shimizu & Chuang 20418 (Taiwan). -***L. oligolepidus*** (Baker) Ching: Cavalerie 34 (China); Henry 2049 (China); Matthew 31 (China). -***L. onoei*** (Franch. & Sav.) Ching: Iwatsuki 1540 (Japan); Iwatsuki et al. 5566 (Japan); Ohba 662598 (Japan). -***L. preussii*** (Hieron.) Pic.Serm.: Brunt 764 (Cameroon); Chapman 62 (Nigeria); Saxer 13 (Cameroon). -***L. pseudonudus*** Ching: Luo 237(64) (China); Wilson 2633 (China). -***L. pseudo-ussuriensis*** Tagawa: Faurie 591(China), 644 (China); Tagawa s.n. (China). -***L. schraderi*** (Mett.) Ching: Chase 6568 (Rhodesia); Loveridge 392 (Uganda); Pichi Sermolli, P. 5141 (Tanzania). -***L. scolopendrium*** (Ching) Mehra & Bir: Gamble 8212 (India); Hancock 104 (China); Smitinand et al. 1744 (Thailand). -***L. sesquispedalis*** (J.Sm.) Fraser-Jenkins (= ***L. scolopendrium*** (Ching) Mehra & Bir): Chola Rangle 4399 (India); Duthie 5183 (India); Kari 176 (China). -***L. subconfluens*** Ching: Hennipman 3141 (Thailand); Rock 8727 (China); Snitinand 4667 (Thailand). -***L. sublinearis*** (Baker ex Takeda) Ching: Hancock 83 (China); Henry 9062A (China); Tagawa et al. 2878 (Thailand). -***L. thunbergianus*** (Kaulf.) Ching: Cox et al. 198 (China); Taquet 3656 (Korea); Wilson 53179 (China). -***L. tosaensis*** (Makino) H.Ito: Tagawa & Iwasuki 3716 (Japan). -***L. ussuriensis*** (Regel & Maack) Ching: Furuse 7138 (Japan); Komrov 46 (China); Tagawa 764 (Japan). -***Neocheiropteris ensata*** Ching: Tagawa and Iwasuki 539 (Japan); Gustav Mann. s.n. (India); Tagawa,Togashi and Kanoi s.n. (Japan). -***N. palmatopedata*** Christ: Beauvais 830 (China); Chang 808 (China); Kokonor Tibet complex expedition 13339 (China); Qin 83 (China). -***Paragramma balteiformis*** (Brause) Hovenkamp: Brass 23289 (Papua New Guinea), 12075 (Papua New Guinea). -***P. longifolia*** (Blume) T. Moore: Boonkerd 1191 (Thailand); Cadière 791 (Vietnam); Edano 35625 (Philippines). -***Platygyria inaequibasis*** Ching & S.K.Wu: Li & Wang 20658 (China); Wu et al. 75-771 (China); Zhang (Dian team) 1753 (China). -***P. soulieana*** (Christ) X.C. Zhang & Q.R. Liu: Delavay 207/1 (China); Li 3 (China). -***P. variabilis*** Ching & S.K.Wu: Ching 23475 (China); Chu & Feng, 747 (China); Sykes & Williams 3503 (Nepal). -***P. waltonii*** (Ching) Ching & S.K.Wu: Littledale s.n. (China); Tibetean team 74-3626 (China); Walton s.n.(China).

Appendix II. A list of 26 quantitative characters with unit or character states used in the study of *Lepisorus* and its related genera.

Abbreviation	Characters
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
RSLE	rhizome scale length in mm
RSWI	rhizome scale width in mm
STL	stipe length in mm
STD	stipe diameter at the middle of its length in mm
PHL	phyllopodia length in mm
PHD	phyllopodia diameter at the middle of their length in mm
LL	lamina length in mm
LW	lamina width in mm

Abbreviation	Characters
LASL	length of the apical sterile portion of lamina in mm
SL	sorus length in mm
SW	sorus width in mm
LFPL	length of the fertile portion of lamina in mm
SPOL	sporangium length in µm
SPOW	sporangium width in µm
AW	annulus width in µm
SPL	spore length in µm
SPW	spore width in µm
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
LLLF	ratio of lamina length and length of fertile portion

Appendix III. A list of 27 qualitative characters with unit or character states used in the study of *Lepisorus* and its related genera.

Abbreviation	Characters
RHS	rhizome surface: not glaucous (0), glaucous and not glaucous (1), glaucous (2)
RSA	apex of rhizome scale: obtuse (0), obtuse and acute (1), acute and acuminate (2), filiform (3)
RSB	base of rhizome scale: obtuse and round (0), obtuse and round and cordate (1), cordate (2)
RSM	margin of rhizome scale: entire (0), entire, dentate and denticulate (1), dentate and denticulate (2)
RSS	shape of rhizome scale: lanceolate and triangular and ovate (0), circular, lanceolate, triangular and ovate (1)
RSCL	clathrate appearance of rhizome scale: clathrate throughout (0), center clathrate with non clathrate margin (1), center clathrate with non clathrate margin, and center opaque with clathrate or non clathrate margin (2), center opaque with clathrate and non clathate margin (3)
RSOR	orientation of rhizome scale: appressed (0), appressed and slightly spreading (1), slightly spreading (2), strongly spreading (3)
RSCO	colour of rhizome scale: one colour (0), one and two colours (1), two colours (2)
RSAT	attachment type of rhizome scale: all scale basifixed (0), pseudopeltate, basifixed and 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 and close to base more than apex (0), at base, at the middle and close to base more than apex (1)
LI	lamina indentation: margin entire and undulate (0), auriculate (1), hastate and pedatifid (2)
LA	lamina apex: acute (0), acute and acuminate (1), acute, acuminate, obtuse and round (2), acute, obtuse and round (3), acuminate (4), acuminate, obtuse and round (5), obtuse and round (6)
LT	lamina texture: membranaceous and chartaceous (0), membranaceous, subcoriaceous and coriaceous (1), subcoriaceous and 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)
ADL	adaxial surface of lamina: lamina glabrous (0), lamina glabrous and 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)

Abbreviation	Characters
LV	veins or lateral vein prominence on abaxial surface of lamina: inconspicuous (0), inconspicuous and conspicuous (1), conspicuous (2)
LBS	symmetry of lamina base: symmetric and nearly symmetric (0), present both symmetric and asymmetric base (1)
SODBA	sori distribution between lamina base and apex: only on upper half (0), on upper half and 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 and more than one row (1), more than one row (2)
SOPO	sorus position between midrib 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)
SOR	sori orientaion when compare with the closest midrib: not oblique (0), present both oblique and not oblique sori (1), oblique (2)
STOP	stomium position: at the position between the thin wall epi- and hypostomium (0), not constantly positioned on annulus (1)
INDC	occurrence of indurate cells: more than half of annulus are indurate cells (0), indurate cell of annulus 1-5 or less than 1/5 of annulus or absent (1)
BALV	large vein at lamina base: absent (0), present (1)