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Phenetic study of the genus *Thelypteris* in Thailand

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ABSTRACT: *Thelypteris* Schmidel s.l. is a genus of the Thelypteridaceae. It comprises about one thousand species, and mostly occurs in tropical and subtropical regions of the world. Up to now, the genera within the Thelypteridaceae have not been clearly classified due to significantly differing taxonomic concepts of pteridologists. Some authors have placed all species in a single genus, whilst others have segregated *Thelypteris* s.l. into two or more genera. In Thailand, *Thelypteris* s.l. is commonly found in various habitats throughout. Fifty one species have been reported and were classified into two genera. In contrast, these same species would be classified into 16 genera according to Holttum's classification. In order to clarify this taxonomic inconsistency, 518 operational taxonomic units (OTUs) from 27 species were analysed using cluster and canonical discriminant analyses. A total of 21 quantitative and 11 qualitative characters were employed. In cluster analysis using only quantitative characters, the 518 OTUs could be separated into three groups or genera, i.e., *Thelypteris* s.s., *Macrothelypteris*, and *Pronephrium*, at an average taxonomic distance of 1.50. The same result was obtained when both quantitative and qualitative characters were used. Canonical discriminant analysis also indicated that there were three groups within the genus *Thelypteris* s.l. The three groups/genera can be distinguished on the basis of scale width, angle of basal pinnae to rachis, number of annulus cells, spore height, and spore diameter. In all, the results from this phenetic study support the segregation of *Thelypteris* s.l. into three genera, viz. *Thelypteris* s.s., *Macrothelypteris*, and *Pronephrium*.

KEYWORDS: Thelypteridaceae, *Macrothelypteris*, *Pronephrium*, cluster analysis, canonical discriminant analysis

INTRODUCTION

Thelypteridaceae is one of the largest families of seedless vascular plants, comprising nearly a thousand species mostly in tropical and subtropical regions with less than 2% found in temperate regions. Diagnostic characters of the family Thelypteridaceae include the possession of two meristeles throughout the length of the stipe (compared to many meristeles in Dryopteroid ferns) and the presence of acicular hairs on many parts of the fronds. Spores are bilateral with a prominent perispore. Chromosome base numbers of Thelypteridaceae range from 27 to 36[1]. In contrast, those of its related groups, i.e., Dryopteroids and Athyrioids, have 40 and 41 as their chromosome base numbers, respectively.

Until now, the Thelypteridaceae have not been clearly classified, with the result that some genera are included or excluded from this fern family due to differing concepts applied by various pteridologists. So far, the treatment concerning the circumscription and relationship of the thelypteroid ferns are those given by Christensen[2], Copeland[3], Ching[4], Morton[5], Iwatsuki[6] and Holttum[7]. Some authors, for example Morton[5] treated all species as a single genus, i.e., *Thelypteris* Schmidel, whilst the others segregated the genus *Thelypteris* s.l. into two to more genera, for example Christensen[2], Ching[4], Iwatsuki[6], and Holttum[7].

The Thelypteridaceae are commonly found throughout Thailand. Fifty one species were reported and classified as belonging to two genera, viz. *Thelypteris* and *Meniscium*[8], while Boonkerd and Pollawatn[9] proposed a segregation of *Thelypteris* s.l. into 14 genera. From even this limited example it can be seen that classification within the Thelypteridaceae so far is not clear and is waiting for re-investigation.

MATERIALS AND METHODS

Specimen collections

The 518 specimens of *Thelypteris* s.l. species were collected from their natural habitats (Table 1). They were identified using the key to species in the Flora of Thailand[8]. Corresponding taxa according to Holttum's classification[7] were also determined. Then they were confirmed by comparing to the voucher specimens deposited at BCU, BKF, E, L, P, and K (Herbarium abbreviations according to Holmgren and Holmgren[10]).

Table 1 Twenty seven taxa of *Thelypteris* s.l. used in multivariate analyses. A: *Thelypteris* s.s., B: *Macrothelypteris*, C: *Pronephrium*.

Botanical Name[8]	Corresponding taxa after Refs. 7, 11	No. of OTUs	This study
Meniscium proliferum (Retz.) Sw.	*Ampelopteris prolifera* (Retz.) Copel.	30	A
Thelypteris arida (D. Don) C. V. Morton	*Christella arida* (D. Don) Holttum	10	A
Thelypteris ciliata (Wall. ex Benth.) Ching	*Trigonospora ciliata* (Wall. ex Benth.) Holttum	30	A
Thelypteris confluens (Thunb.) C. V. Morton	*Thelypteris confluens* (Thunb.) C. V. Morton	10	A
Thelypteris crassifolia (Blume) Ching	*Mesophlebion crassifolium* (Blume) Holttum	10	A
Thelypteris crinipes (Hook.) K. Iwats.	*Christella crinipes* (Hook.) Holttum, B. Nayar & Kaur	10	A
Thelypteris dentata (Forssk.) St. John	*Christella dentata* (Forssk.) Brownsey & Jermy	30	A
Thelypteris falciloba (Hook.) Ching	*Pseudocyclosorus falcilobus* (Hook.) Ching	30	A
Thelypteris ferox (Blume) Tagawa & K. Iwats.	*Chingia ferox* (Blume) Holttum	10	A
Thelypteris flaccida (Blume) Ching	*Metathelypteris flaccida* (Blume) Ching	10	A
Thelypteris hirsutipes (Clarke) Ching	*Coryphopteris hirsutipes* (Clarke) Holttum	10	A
Thelypteris hirtisora (C. Chr.) K. Iwats.	*Sphaerostephanos hirtisorus* (C. Chr.) Holttum	30	A
Thelypteris interrupta (Willd.) K. Iwats.	*Cyclosorus interruptus* (Willd.) H. Ito	30	A
Thelypteris larutensis (Bedd.) Tagawa & K. Iwats.	*Sphaerostephanos larutensis* (Bedd.) C. Chr.	10	A
Thelypteris megaphylla (Mett.) K. Iwats.	*Sphaerostephanos penniger* (Hook.) Holttum	30	A
Thelypteris nudata (Roxb.) C. V.Morton	*Pronephrium nudatum* (Roxb.) Holttum	30	C
Thelypteris polycarpa (Blume) K. Iwats.	*Sphaerostephanos polycarpus* (Blume) Copel.	30	A
Thelypteris repanda (Fée) Tagawa & K. Iwats.	*Pronephrium repandum* (Fée) Holttum	10	C
Thelypteris siamensis Tagawa & K. Iwats.	*Christella siamensis* (Tagawa & K. Iwats.) Holttum	10	A
Thelypteris singalanensis (Baker) Ching	*Metathelypteris singalanensis* (Baker) Ching	10	A
Thelypteris sumatrana (v.A.v.Ros.) K. Iwats.	*Pseudophegopteris sumatrana* Holttum	10	B
Thelypteris terminans (Hook.) Tagawa & K. Iwats.	*Amphineuron terminans* (Hook.) Holttum	30	A
Thelypteris torresiana (Gaud.) Alston	*Macrothelypteris torresiana* (Gaud.) Ching	30	B
Thelypteris truncata (Poiret) K. Iwats.	*Pneumatopteris truncata* (Poiret) Holttum	18	A
Thelypteris viscosa (Baker) Ching	*Coryphopteris viscosa* (Baker) Holttum	10	A
Thelypteris xylodes (Kunze) Ching	*Pseudocyclosorus xylodes* (Kunze) Ching	10	A
Thelypteris sp.	*Trigonospora* sp.	30	A
(2 genera)	(19 genera)	518	

Table 2 Twenty one quantitative characters of fertile fronds used in multivariate analyses of *Thelypteris* s.l. with their methods of scoring.

Character	Details of measurements and counts
scale width	width of scale at base of stipe in mm
scale length	length of scale at base of stipe in mm
stipe length	length of stipe in mm
rachis length	length of rachis in cm
basal pinnae width	width of basal pinnae in cm
basal pinnae length	length of basal pinnae
angle of basal pinnae to rachis	-
number of pinnae per frond	-
distance between pairs of the largest pinnae	distance in cm
lateral pinnae width	width of the largest lateral pinnae in cm
lateral pinnae length	length of the largest lateral pinnae in cm
pinnae lobe depth	perpendicular distance between margin and base of lobe in mm
number of sori per lobe	number of sori per lobe of the largest lateral pinnae
lateral vein length (cm)	length of lateral veins of the largest lateral pinnae in cm
number of pairs of lateral veins per pinna	-
sporangium width (mm)	the longest distance measured from side to side of sporangium at the equatorial axis in mm
sporangium length (mm)	the longest distance measured from base to top of sporangium (without stalk) in mm
number of annulus cells	number of annulus cells per sporangium
stalk length (mm)	length of sporangium stalk in mm
spore height (mm)	height of spore from lateral view in mm
spore diameter (mm)	diameter of spore from lateral view in mm

Character measurements

In total, 21 quantitative and 11 qualitative characters of the collected specimens were studied and selected for multivariate analyses (Tables 2 and 3). Measurements of morphological characters were carried out on fertile fronds. Linear measurements of macroscopic characters were performed using a standard ruler or a digital caliper. Microscopic characters were measured with the aid of a light microscope equipped with 10 × lens coupled to a micrometer disc and 10 × or 40 × objectives.

Table 3 Eleven qualitative characters of fertile fronds used in multivariate analyses of *Thelypteris* s.l. with their methods of scoring.

Character	Details of measurements and counts
form of rhizome	erect (1), suberect (2), short creeping (3), long creeping (4)
buds on rachis	absent (0), present (1)
basal pinnae	not or slightly reduced (1), extremely reduced (2), suddenly reduced to form butterfly shaped auricles (3)
form of frond	once-pinnate (1), bi-pinnate-tri-pinnatifid (2)
upper-surface of costae	not grooved (0), grooved (1)
margin of pinnae	subentire (1), pinnae lobed less than half way to costae (2), pinnae lobed to half way towards costae (3), pinnae always deeply lobed (4)
venation pattern	vein free (1), vein anastomosing (2), vein in several pairs all anastomosing and joining to form zigzag composite vein alternating with the costules (3)
sori	exindusiate (0), indusiate (1)
acicular hairs or glandular hairs on sporangium	absent (0), present (1)
acicular hairs or glandular hairs on sporangium stalk	absent (0), present (1)
spore type	monolete (1), trilete (2)

Data analyses

Cluster analyses and canonical discriminant analysis were performed to determine the pattern of grouping of the collected specimens. Cluster analysis was performed when only quantitative characters were used. The original data matrices were standardized and the resultant matrix was used to produce the distance matrix based on average taxonomic distance. Then, cluster analyses were conducted using the unweighted pair-group method with arithmetic (UPGMA) in SAHN. These procedures are available in NTSYS-pc version 2.11S[12]. When mixed characters, i.e., quantitative and qualitative morphological characters were measured altogether, the Gower similarity coefficient was calculated and clustered by the group-average method as suggested by Gower[13]. The statistics package, MVSP (Kovach Computing Services, MVSP Plus, version 3.1[14]) was used. Canonical discriminant analysis was performed with SPSS for Windows[15]. Stepwise discriminant analysis was used to select a subset of characters that maximized differences among the groups determined by cluster analysis. Correct classification rates were used as indicators of separation among the groups. To summarize the range of variation between and within the segregated groups on each character, univariate analysis was performed[15].

RESULTS AND DISCUSSION

Cluster analysis

In the cluster analysis, resemblance coefficient matrices were produced. The first matrix was the average taxonomic distance derived from 21 quantitative characters and the second one was the Gower's similarity coefficient matrix derived from 21 quantitative characters plus 11 qualitative characters.

The results of the first cluster analysis using the average taxonomic distance matrix is shown in Fig. 1. The dendrogram splits the 518 specimens into three groups (Group A–C) at the average taxonomic distance of 1.50. The first group (A) consisted of 23 species (*Meniscium proliferum*, *Thelypteris arida*, *T. ciliata*, *T. confluens*, *T. crassifolia*, *T. crinipes*, *T. dentata*, *T. falciloba*, *T. ferox*, *T. flaccida*, *T. hirsutipes*, *T. hirtisora*, *T. interrupta*, *T. larutensis*, *T. megaphylla*, *T. polycarpa*, *T. siamensis*, *T. singalanensis*, *T. terminans*, *T. truncata*, *T. viscosa*, *T. xylodes*, *Thelypteris* sp.). The second group (B) comprised of two taxa, namely, *T. torresiana* and *T. sumatrana*. The third group (C) included the two species *T. nudata*, and *T. repanda*.

Similar results were obtained when both quantitative and qualitative characters were used. The dendrogram derived from the second cluster analysis is shown in Fig. 2. Using the 70% similarity phenon line as a reference[16], three main groups could be distinguished in the UPGMA phenogram. Members of the three groups (Group A–C) were the same as those of the three groups obtained from the first cluster analysis.

In group A, there were 13 genera according to Holttum's classification[7,11]. They are *Ampelopteris*, *Amphineuron*, *Chingia*, *Christella*, *Coryphopteris*, *Cyclosorus*, *Metathelypteris*, *Mesophlebion*, *Pneumatopteris*, *Pseudocyclosorus*, *Sphaerostephanos*, *Thelypteris*, and *Trigonospora*. Holttum[7,11] used a combination of characters to distinguish the 13 mentioned genera. In contrast, according to Tagawa and Iwatsuki[8], 23 species of group A were subdivided into 22 species of *Thelypteris* and one species of *Meniscium* (Table 1). They used a proliferous character of

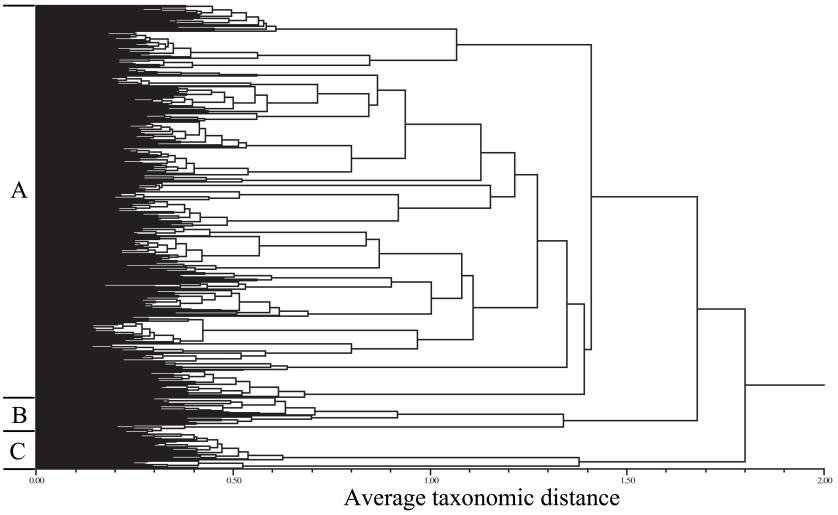

Fig. 1 UPGMA clustering of 518 OTUs based on 21 characters of *Thelypteris* s.l. in Thailand.

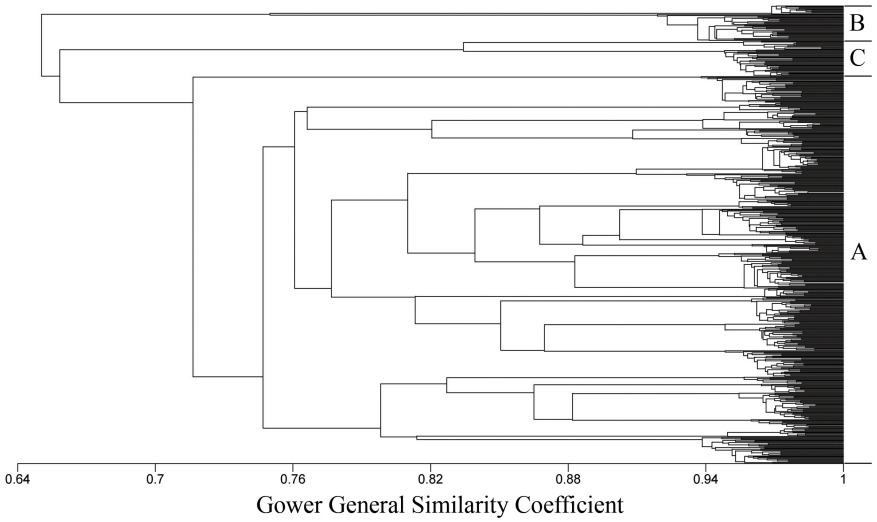

Fig. 2 UPGMA phenogram base on Gower's general similarity coefficient calculated between means of 21 quantitative and 11 qualitative morphological characters of the genus *Thelypteris* s.l. in Thailand.

rachis to separate *Meniscium* from *Thelypteris*. In the light of both cluster analyses, it is evident that group A should be classified into only one taxon, preferably the genus *Thelypteris*, since the type genus *Thelypteris* is in this cluster and this taxon name has higher priority than the others. From a close examination of a dendrogram in Fig. 2, it appears that two subclusters could be established. Subcluster 1 comprised of *T. prolifera*, corresponding to *Ampelopteris* sensu Holttum or *Meniscium* sensu Tagawa and Iwatsuki. It is noteworthy that both authors used the same characters to classify this taxon, i.e., proliferous character on rachis. The other cluster contained the remaining 12 genera as mentioned earlier.

Two taxa in group B conformed to the genera *Pseudophegopteris* and *Macrothelypteris* according to Holttum's classification[7]. Holttum recognized these two genera based on characters of scales on fronds and spore morphology. However, Pichi Sermolli[17] recognized only one genus, and transferred all species of *Pseudophegopteris* to *Macrothelypteris*. Unification of these two genera was based on bi-pinnate fronds. It

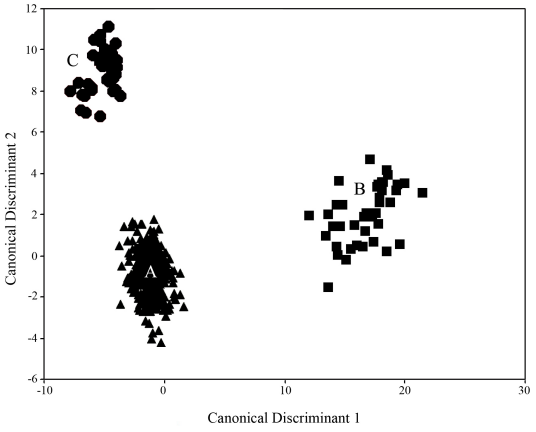

Fig. 3 Ordination plot of 518 specimens from 27 taxa of *Thelypteris* s.l. in Thailand based on 21 quantitative characters.

is evident that the results of cluster analyses from our study support Pichi Sermolli's classification.

All OTUs in group C were members of the genus *Pronephrium* sensu Holttum. Holttum[7] used the venation pattern as an important character to separate the genus *Pronephrium* from the other genera in his classification. He noted that when pinnae lobes are not deep, veins from adjacent costules joined to form an excurrent straight or zigzag vein. These united veins run to the translucent membrane at the base of a sinus between the two lobes[7]. It can be seen that the results of cluster analyses clearly support the separation of the genus *Pronephrium* from the majority of *Thelypteris* s.l.

In all, the results of cluster analyses supported the recognition of the three genera, i.e., *Thelypteris* s.s., *Macrothelypteris*, and *Pronephrium*.

Canonical discriminant analysis

In canonical discriminant analysis, 21 characters were evaluated by stepwise discriminant analysis to determine which characters are important in discriminating among these three groups as suggested by cluster analyses. Out of the 21 characters, all except 3 and 8 were selected as important characters in giving the best separation of the groups (Table 4). In addition, the specimens were correctly classified into the respective group (A, B, or C) with 100% accuracy. These classification rates are extremely high considering the existing variations among the three groups. The result was the same when the original group (27 taxa) was used a priori in canonical discriminant analysis, i.e., it yielded 3 groups in an ordination plot (Fig. 3).

The ordination plot of the 518 OTUs was presented on the two canonical axes (Fig. 3). It can be seen that group B is clearly separated from groups A and C on canonical axis 1. Likewise, group C is evidently separated from group A and B on canonical axis 2. So the three groups appear distinct. Canonical variable 1 (axis 1) is most highly influenced by five characters (Table 4), viz. scale width, angle of basal pinnae to rachis, number of annulus cells, spore height and spore diameter. The canonical correlation of the first canonical discriminant function is 98% with all the variables and the variance explained by it is 77%. Thus, these two axes are effective for separating the three morphological groups of the genus *Thelypteris* s.l. in Thailand.

From the ordination plot in Fig. 3 it can be seen that group B was rather heterogeneous, whereas group C and group A were less variable.

It can be concluded that cluster analyses and canonical discriminant analyses from this study do not support a separation of *Thelypteris* s.l. in Thailand into either 2 or 16 genera (Table 1) according to Holttum's classification[7,11]. Instead, the results from this study support the separation of *Thelypteris* s.l. in Thailand into 3 genera, i.e., *Thelypteris* s.s., *Macrothelypteris* and *Pronephrium* based on both quantitative and qualitative characters. Corresponding results were presented by Smith and Cranfill[18]. They recognized 5 genera, namely *Macrothelypteris*, *Pseudophegopteris*, *Phegopteris*, *Thelypteris* s.s., and *Cyclosorus* sensu Smith, based on data from four chloroplast genes (*rps*4 gene + *rbc*L gene + *trn*S spacer, + *trn*L spacer; 2600 base pairs) of specimens from 23 genera according to Holttum's classification. They note that their sampling was as yet insufficient to favour one classification over another. It is pertinent to note that the present analysis suggested that recognition of an intermediate number of genera may be the most suitable for classification in Thelypteridaceae.

Important characters

Univariate analysis of 21 quantitative characters was performed (Table 4). It was found that there were statistically significant differences ($p < 0.05$) in all characters among the three proposed genera, viz. *Thelypteris*, *Macrothelypteris*, and *Pronephrium*. The F-values (Table 4) indicate by their magnitude the relative order of importance of the characters in general. It is clear that the F-values almost reflect the association of characters with canonical axis 1 because of its high correlation and high variance. Basic statistics of the three proposed genera are also summarized in Table 4. It can be concluded that the vegetative characters

Table 4 Pooled results within canonical structure of 3 groups taxa (A–C) according to the results of canonical discriminant analysis; F-values, means and standard errors of 21 quantitative characters of the three genera.

				Thelypteris s.s.		*Macrothelypteris*		*Pronephrium*	
Character	Axis 1	Axis 2	F-value	mean	± SE	mean	± SE	mean	± SE
scale width	0.018*	0.004	3.41	0.99	0.02	0.80	0.01	0.99	0.03
scale length	0.022	0.053*	4.651	7.12	0.22	8.99	0.29	8.469	0.34
stipe length	−0.026	0.165*	64.37	34.69	1.05	42.96	2.13	73.299	1.42
rachis length	−0.020	0.081*	12.64	78.03	3.12	62.29	1.41	125.39	8.03
basal pinnae width	0.306	0.448*	1389.03	1.21	0.02	8.20	0.38	3.65	0.07
basal pinnae length	0.064	0.243*	180.64	6.95	0.34	21.17	0.97	24.11	0.47
angle of basal pinnae to rachis	0.038*	0.020	9.10	109.43	41.79	136.25	0.56	107.00	1.76
no. of pinnae per frond	−0.003	0.106*	11.21	53.32	1.87	34.90	1.27	30.25	1.91
distance between the pair of the largest pinnae	0.015	0.190*	73.81	1.12	0.04	2.13	0.33	2.91	0.13
lateral pinnae width	0.269	0.428*	1086.86	1.68	0.03	8.40	0.35	4.45	0.06
lateral pinnae length	0.025	0.154*	50.75	14.98	0.43	22.20	0.89	27.73	0.60
pinnae lobe depth	0.081	0.171*	78.59	4.01	0.09	5.60	0.09	1.05	0.03
no. of sori per lobe	−0.156	0.232*	358.85	10.77	0.24	3.17	0.61	30.70	0.78
lateral vein length	−0.086	0.349*	373.74	0.86	0.02	0.70	0.09	2.42	0.06
no. of pairs of lateral veins per pinna	−0.114	0.228*	241.80	35.64	0.77	17.32	0.43	84.77	0.84
sporangium width	0.067	0.187*	80.27	0.19	0.001	0.21	0.001	0.13	0.01
sporangium length	0.050	0.210*	74.18	0.24	0.002	0.25	0.001	0.15	0.01
no. of annulus cells	0.075*	0.019	37.46	15.01	0.09	17.27	0.28	14.80	0.13
stalk length	0.004	0.094*	17.53	0.19	0.003	0.17	0.01	0.12	0.01
spore height	0.042*	−0.020	13.20	0.03	0.000	0.03	0.001	0.09	0.000
spore diameter	0.099*	0.076	81.38	0.04	0.000	0.05	0.001	0.04	0.000

* denotes largest absolute correlation between each character and any discriminant function

Table 5 Key to the genera of Thelypteridaceae in Thailand.

1a Frond 2–3 pinnate; number of annulus cells equal to or more than 17 ... **1. *Macrothelypteris***
1b Frond 1-pinnate; number of annulus cells less than 17
  2a Spore height less than 0.05 mm ... **2. *Thelypteris***
  2b Spore height more than 0.05 mm ... **3. *Pronephrium***

of *Thelypteris* s.s. and *Pronephrium* were generally larger than those of *Macrothelypteris*. In contrast, the reproductive characters of *Macrothelypteris* were larger than those of *Thelypteris* and *Pronephrium*.

CONCLUSIONS

Thelypteris s.l. is a large and complex genus comprising about 1000 species and being a single genus in the family Thelypteridaceae[19], since its academic separation from the dryopteroid ferns about 60 years ago. Although generally recognized as a natural monophyletic group, there are still some differences in opinion among pteridologists on generic circumscription.

This study was focused on numerical taxonomy. 518 specimens (OTUs) from 27 species of *Thelypteris* s.l. in Thailand were subjected to cluster analyses and canonical discriminant analysis. Based on 21 quantitative characters and supported by 11 qualitative characters, cluster analysis strongly indicates the presence of three distinct groups, i.e., *Thelypteris* s.s., *Macrothelypteris*, and *Pronephrium*. The 3 groups were subsequently evaluated by canonical discriminant analyses. It was found that 5 characters, i.e., scale width, angle of basal pinnae to rachis, number of annulus cells, spore height and spore diameter collectively supported the segregation of 3 groups or genera from the *Thelypteris* s.l.

Table 5 is an identification key of the segregated genera from the *Thelypteris* s.l. in Thailand.

In summary, numerical taxonomy may be used effectively alongside traditional methods of logical

analysis in taxonomy, as shown clearly in the proposed classification. However, the results of this phenetic methods do not reflect phylogenetic relationships and require careful interpretation. Though these computerized analytical techniques have proved to be decisively useful in classification of *Thelypteris* s.l. in Thailand.

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