A Revised Framework of *Dryopteris* subg. *Nothoperanema* (Dryopteridaceae) Inferred from Phylogenetic Evidence, with Descriptions of Two New Sections

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Abstract—Dryopteris subgenus Nothoperanema (Dryopteridaceae) includes sections Acrophorus, Diacalpe, Nothoperanema, and Peranema. Phylogenetic relationships among these sections and their relationship to sect. Dryopsis (genus Dryopteris subgenus Erythrovariae, Dryopteridaceae) are unclear. Additionally, previous phylogenetic work has not included Stenolepia, which has been suggested as an important relative of Peranema based on morphology. In this study, we examined phylogenetic relationships within subgenus Nothoperanema by including Stenolepia and utilizing six plastid regions (~5,500 characters). Our inferred phylogeny revealed that sect. Dryopsis is not monophyletic. The Nothoperanema clade is highly supported, and includes sect. Acrophorus, sect. Diacalpe, sect. Nothoperanema, sect. Peranema, certain Dryopsis species, and Stenolepia. By re-examining diagnostic morphological characters, we establish and describe two new sections under subgenus Nothoperanema: sect. Shiehia and sect. Stenolepia. This revision accommodates new species transferred from sects. Dryopsis and Stenolepia, and makes subgenus Nothoperanema and each of its sections natural groups. Finally, we provide a table with morphological comparisons and a key to sections.

Keywords—Acrophorus, Diacalpe, Dryoptis, Shiehia, Peranema, Stenolepia.

Dryopteris subgenus Nothoperanema Tagawa was first established by Tagawa (1938) within Dryopteridaceae, and was later raised to genus level (as Nothoperanema) within Dryopteridaceae (Ching 1966). This subgenus differs from others in Dryopteris by bearing hair-like scales (i.e. Holttum and Edwards 1986; Widén et al. 2001; or setae, cf. Zhang et al. 2013) on the adaxial surface of laminae (Fig. 1A; Tagawa 1938; Ching 1966; Kramer et al. 1990; Wu and Ching 1991; Zhang et al. 2013). Based on phylogenetic evidence, Peranema D. Don, Diacalpe Blume, and Acrophorus C. Presl were also included in this subgenus as different sections (Zhang and Zhang 2012). These three genera have been treated as distinct group(s) within the Dryopteridaceae because their sori are more or less enclosed and wrapped by inferior indusia (Kramer et al. 1990). Peranema is characterized by its stalked sori, which is enclosed in a spherical indusium and suspended by an elongated and vascularized sporophore (stalk) underneath the abaxial surface of fertile leaves (Fig. 1F). Diacalpe is similar to Peranema but has sessile sori without sporophores (Fig. 1E). Acrophorus differs from the other two genera in having hemispherical sori. Because of their distinctive soral morphology, these three genera have complex taxonomic histories; for example, they have been recognized together as comprising an independent family, Peranemaceae (Ching 1940). Recently, they were revealed to have close relationships with Nothoperanema and certain species of Dryopsis Holttum & Edwards that have round or reniform superior indusia (Li and Lu 2006; Liu et al. 2007; Ebihara 2011; McKeown et al. 2012). Dryopsis is phylogenetically imbedded in Dryopteris (Li and Lu 2006; Liu et al. 2007; Ebihara 2011; McKeown et al. 2012; Zhang and Zhang 2012). Most recently, Dryopsis species have been assigned to Dryopteris subgenus Erythrovariae sect. Dryopsis (Zhang 2012).

The relationships between Nothoperanema and its allies including Dryopsis remain unclear. These unresolved relationships may result from insufficient phylogenetic information; some of the phylogenetic inferences were based on only one or two genetic regions (e.g. Li and Lu 2006; Liu et al. 2007; Ebihara 2011). Additionally, some previous phylogenies implied conflicting relationships (Li and Lu 2006; Liu et al. 2007; Ebihara 2011; McKeown et al. 2012; Zhang and Zhang 2012; Zhang et al. 2012). For example, Dryopteris maxinovicziana (Miq.) C. Chr. [i.e. Dryopteris maxinovicziana (Miq.) Holttum & P. J. Edwards or Clenitis maxinovicziana (Miq.) Ching] was alternatively resolved as sister to Acrophorus + Nothoperanema or nested in Nothoperanema (Ebihara 2011; McKeown et al. 2012), but also shown as being distantly related to Acrophorus + Nothoperanema + Diacalpe + Peranema in another study (Zhang et al. 2012). None of the current phylogenetic work includes Stenolepia Alderw., which has been suggested as an important relative of Peranema based on morphology (Holttum and Edwards 1986; Kramer et al. 1990).

To resolve the relationships of Nothoperanema and its relatives, this study utilizes not only non-coding regions (rps16-matK IGS, ndhF-trnN, and trnL-F region), but also rapidly evolving coding regions (matK, ndhF, and chlF) that have been applied to overcome similar difficulties in other fern phylogenies (Kuo et al. 2011; Rothfels et al. 2012; Shinohara et al. 2013), for phylogenetic analyses. We include Stenolepia, Dryopsis species, and all sections of subg. Nothoperanema in our analyses to avoid any topological uncertainties due to incomplete taxon sampling of represented lineages. Additionally, the diagnostic morphological characteristics
for the Nothoperanema clade, the clade containing subg. Nothoperanema and sister to the Aemulae clade (Zhang et al. 2012), and each lineage within this clade were re-examined. Based on the phylogenetic and morphological evidence, this study further provides a revised framework of Dryopteris subgenus Nothoperanema and a key to identify its infra-subgeneric sections.

**Materials and Methods**

**Phylogenetic Sampling**—A total of 33 Dryopteris species and two outgroups in the two most closely related genera [i.e. Polystichum Roth and Arachniodes Blume (Li and Lu 2006; Liu et al. 2007; Ebihara 2011; McKeown et al. 2012; Zhang et al. 2012)] were included in our phylogenetic analyses. The sampling of Dryopteris species included representatives from each of the major clades revealed in previous analyses using comprehensive taxon sampling (Zhang et al. 2012). Between 27% and 100% of recognized species were sampled for each section in subg. Nothoperanema (sensu Zhang and Zhang 2012, and Zhang and Liu 2014). For sect. Dryopsis, eight of 21 species were sampled (sensu Zhang 2012). We included only one sample of Stenolepia, which is presumably monotypic (Kramer et al. 1990). Voucher information is summarized in Appendix 1.

**Phylogenetic Analyses**—DNA was extracted using a modified CTAB procedure (Wang et al. 2004). Universal and newly designed specific primers were used for amplifying cpDNA regions, including trnL-F (trnL-F IGS + trnL gene), rps16-matK IGS, matK, rpoB, rplF-trnN IGS, and

The PCR reactions were performed in 15 μL reaction volumes, including 20 ng genomic DNA, 1 x PCR buffer, 200 μM dNTP, 15 pmol of each primer, and 0.5 U Taq polymerase (PrioTaq, PROTECH, Taipei, Taiwan) or 0.75 U Phusion polymerase (Finnzymes, Espoo, Finland). Primer information is in Table 1. After sequencing, DNA sequences were aligned by ClustalW implemented in BioEdit v. 7.0.5.3 (Hall 1999) using the default settings. Ambiguously aligned tandem repeats in rps16-matK IGS were removed from the alignments manually. The alignment was deposited in Dryad (http://dx.doi.org/10.5061/dryad.mr076). Aemulae clade (Fig. 2). The tree file was deposited in Dryad (http://dx.doi.org/10.5061/dryad.mzt076).

**Perispore Morphology**—The perispore morphology of all species examined are shown in Fig. 3, and these morphologies are congruent with those described in previous studies (Holttum and Edwards 1986; Tryon and Lugardon 1991; Chen 2007; Lu et al. 2007; Wang and Dai 2010; Ding et al. 2013). The species belonging to subgenus *Nothoperanema* have folded perispores and the folds on perispores are usually reticulate (Fig. 3A–D). *Dryopteris hypolepioides* has such reticulate perispore folds. Three species of sect. *Dryopsis, D. manipurensis, D. maximovicziana, and D. scabrosa*, also have folded perispores but their folds are laminate (Fig. 3F–H). *D. hypolepioides* is the type species of sect. *Dryopsis*, has spiny perispores (Fig. 3I), which are similar to those found in the remaining *Dryopteris* members except for *D. obtusiloba* (Holttum and Edwards 1986; Tryon and Lugardon 1991; Chen 2007; Lu et al. 2007; Wang and Dai 2010; Ding et al. 2013).

**Phylogenetic Patterns**—The relationships among clades in our phylogeny are consistent with previous studies, while relationships within the Nothoperanema clade showed some differences (Geiger and Ranker 2005; Li and Lu 2006; Liu et al. 2012). Based on the rapidly evolving coding regions (i.e. matK, ndhF, and chlL), our inferred phylogeny successfully resolved major relationships within the Nothoperanema clade. The intersection phylogenetic relationships in subg. *Nothoperanema* inferred using these rapidly evolving coding regions alone received higher bootstrap values compared to those resolved using only non-coding regions (data not shown). Additionally, the phylogeny based on these coding regions revealed the same inter-section relationships as the phylogeny inferred using all regions (i.e. non-coding + coding; Fig. 2). This phylogeny strongly suggests the monophyly of sect. *Peranema* + *Diacalpe* + *Acrophorus* (MLBS = 86, PP = 1.00, and MPBS = 100) and sister to the *Aemulae* clade, which was a highly supported monophyletic group (MLBS = 100, PP = 1.00, and MPBS = 100) and sister to the *Diacalpe* clade (Fig. 2). The tree file was deposited in Dryad (http://dx.doi.org/10.5061/dryad.mzt076).

**Results**

**Phylogeny**—The cpDNA alignment matrix of *trnL-L-F* + *rps16-matK* IGS + *matK* + ndhF + ndhF-trnN IGS + chlL comprised a total of 5,473 characters with 1,618 variable sites, which were generated from 35 *Dryopteris* species and two outgroups in Dryopteridaceae. The highest log-likelihood value of the ML tree (Fig. 2) was -20,396.98845. Sect. *Dryopsis* was not monophyletic; species classified in section *Dryopsis* were resolved in the *Dryopsis* and *Nothoperanema* clades separately. In addition to sect. *Nothoperanema, Acrophorus, Diacalpe, and Peranema,* two *Dryopteris* members [i.e. *Dryopteris maximovicziana* and *D. manipurensis* (Bedd.) C. Chr.] and *Stenolepia* (i.e. *Dryopteris hypolepioides* Rosent.) were embedded in the *Nothoperanema* clade, which was a highly supported monophyletic group (MLBS = 100, PP = 1.00, and MPBS = 100) and sister to the *Aemulae* clade (Fig. 2). The tree file was deposited in Dryad (http://dx.doi.org/10.5061/dryad.mzt076).
This relationship was neither resolved nor supported in the previous studies (Li and Lu 2006; Liu et al. 2007; McKeown et al. 2012; Zhang and Zhang 2012; Zhang et al. 2012). Instead, these previous studies inferred an alternative topology showing sect. *Peranema* as sister to sect. *Nothoperanema* + *Diacalpe* + *Acrophorus*. However, with the exception of Zhang et al. (2012), these relationships received only weak support in earlier studies. This latter relationship may have resulted from including *rbcL* sequences in phylogenetic reconstruction as *rbcL* sequences usually contain higher levels of homoplasy (Kuo et al. 2011; Shinohara et al. 2013).

Our phylogeny resolved the phylogenetic positions of *Stenolepia* (i.e. *Dryopteris hypolepioides*) and two *Dryopsis* members (i.e. *D. maximowicziana* and *D. manipurensis*) within the Nothoperanema clade. This is the first phylogenetic analysis in which *D. hypolepioides* and *D. manipurensis* have been included. In previous studies, *D. maximowicziana* was shown to be related to sect. *Nothoperanema* or *Acrophorus* (Ebihara 2011; McKeown et al. 2012). Our phylogeny is consistent with this result; it further shows *D. maximowicziana* resolved with another *Dryopsis* member (*D. manipurensis*) that is also nested in the Nothoperanema clade (Fig. 2). Zhang et al. (2012) inferred the unexpected position of *D. maximowicziana* nested within the Nephrocystis clade instead of Nothoperanema. This seems to have resulted from the inclusion of DNA sequences from misidentified samples, and, indeed, conflicts in phylogenetic positions were found between the phylogeny reconstructed by their *rbcL* sequence (found nested in the Nothoperanema clade; Ebihara 2011) and those reconstructed by their *trnL-L-F* or *rps4-trnS* sequences (found nested in the Nephrocystis clade; data not shown).

**Morphology of the Nothoperanema Clade**—Like other species in the Nothoperanema clade, *Dryopteris hypolepioides*, *D. maximowicziana* and *D. manipurensis* have the following character states: 3-pinnatifid to 5-pinnatifid frond in ovate-triangular shape, stipe scales in broadly lanceolate or subulate shape, and hair-like scales on the adaxial lamina surfaces.

![Fig. 2. The ML phylogeny of the subg. *Nothoperanema* and its relatives. ML bootstrap support (MLBS) values, the posterior probabilities of Bayesian phylogenetic inference (PP), and MP bootstrap support (MPBS) values are indicated on each branch, as MLBS/PP/MPBS. The plus (+) sign represents MLBS = 100, PP = 1.00, or MPBS = 100. The thickened branch indicates MLBS ≥ 70 and PP ≥ 0.95. The gray blocks indicate the section status identified in this study.](image-url)
This combination of character states does not appear in other Dryopteris species, and thus, can provide the morphological basis to distinguish the Nothoperanema clade from the other clades in Dryopteris. In addition, perispores in the Nothoperanema clade are folded and are morphologically different from the spiny perispores of the Dryopsis clade (Fig. 3; Holttum and Edwards 1986; Tryon and Lugardon 1991; Chen 2007; Lu et al. 2007; Wang and Dai 2010; Ding et al. 2013). Among Dryopteris species, the inferior indusium in the Nothoperanema clade is unique and appears only in sect. Acrophorus, Diacalpe, and Peranema. Our phylogeny revealed the monophyly of the clade comprising these three sections (Fig. 2), and further implies a single evolutionary transition from superior to inferior indusia in the genus Dryopteris. A similar transition in indusium position also occurred in Tectariaceae (Moran et al. 2014). Except for sect. Nothoperanema, the members in the Nothoperanema clade have a non-confluent groove at each axis-junction (Fig. 1D). However, this character is homoplastic in Dryopteris, as it also appears in subg. Erythrovariae sect. Dryopsis (Zhang 2012). Morphological comparisons for other informative characters distinguishing sections are shown in Table 2.

**Taxonomic Treatment**

Using current phylogenetic and morphological evidence, we established two new sections in subgenus Nothoperanema to accommodate certain Dryopsis species and Stenolepia, and this revised framework treats subgenus Nothoperanema as a natural lineage. In addition to Dryopteris maximowicziana and D. sphaeropteroides, we recognized an additional four species from subg. Erythrovariae sect. Dryopsis (total 21 species sensu Zhang 2012) and transferred them to the new section under subg. Nothoperanema based on their diagnostic morphological characteristics. Like D. maximowicziana and D. manipurensis, they all have characteristics, such as 2-pinnate-pinnatifid to tririnate fronds in ovate-triangular shape, less densely scaled costae, and much broader scales on basal stipes, differing from the remaining Dryopsis members which have bipinnate, lanceolate fronds (except for Dryopteris ×holtttumii).
<table>
<thead>
<tr>
<th>Section/ Characters</th>
<th>Nothoperanema</th>
<th>Shiehia</th>
<th>Stenolepis</th>
<th>Acrophrous</th>
<th>Discalpe</th>
<th>Peranema</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Morphology of scales on basal stipe</strong></td>
<td>Subulate to lanceolate, brown to dark brown, entire</td>
<td>Lanceolate to ovate-lanceolate, light brown to reddish brown, entire</td>
<td>Lanceolate to broadly lanceolate, brown to dark brown, entire</td>
<td>Ovate-lanceolate to ovate, reddish brown or castaneous, entire, undulate, or toothed</td>
<td>Lanceolate to broadly lanceolate, castaneous to dark red, entire</td>
<td>Subulate to ovate-lanceolate, light brown to dark brown, margins entire or with some clavate, short hairs</td>
</tr>
<tr>
<td><strong>Patterns of scales relative to axis surfaces</strong></td>
<td>Patent</td>
<td>Patent or nearly so at least on half lower portions of stipes</td>
<td>Appressed, ascending or sometimes reflexed</td>
<td>Appressed, ascending or sometimes reflexed</td>
<td>Appressed, ascending or sometimes reflexed</td>
<td>Patent or nearly so</td>
</tr>
<tr>
<td><strong>Frond outline</strong></td>
<td>Ovate or ovate-triangular 3-pinnate to 4-pinnatifid</td>
<td>Ovate or ovate-triangular 3-pinnate to 5-pinnatifid</td>
<td>Ovate or ovate-triangular 3-pinnate to 4-pinnatifid</td>
<td>Ovate or oblong-ovate 3-pinnate to 4-pinnatifid</td>
<td>Ovate or oblong-ovate 3-pinnate to 4-pinnatifid</td>
<td>Catadromous except the most proximal pairs of pinna (anadromous)</td>
</tr>
<tr>
<td><strong>Frond dissection</strong></td>
<td>Catadromous except the most proximal pairs of pinna (anadromous)</td>
<td>Poecilodromous; anadromy, catadromy or isodromy</td>
<td>Catadromous or nearly isodromous except the most proximal pairs of pinna (anadromous)</td>
<td>Catadromous except the most proximal pairs of pinna (anadromous)</td>
<td>Catadromous except the most proximal pairs of pinna (anadromous)</td>
<td>Catadromous except the most proximal pairs of pinna (anadromous)</td>
</tr>
<tr>
<td><strong>Axis dromy</strong></td>
<td>Subulate to lanceolate scales, subulate ctenitis hairs, and slightly longer setae or hair-like scales</td>
<td>Lanceolate scales, contorted subulate ctenitis hairs, and short conical setae</td>
<td>Linear-lanceolate small scales, contorted subulate ctenitis hairs, and short conical setae</td>
<td>Subulate ctenitis hairs and short conical setae; often with a cordate, brown large scale at base of each junction of pinna and pinnule</td>
<td>Subulate small scales, contorted subulate ctenitis hairs, short conical setae</td>
<td>Subulate to lanceolate scales, subulate ctenitis hairs, and short conical setae</td>
</tr>
<tr>
<td><strong>Frond indument</strong></td>
<td>Most of axis-junctions clearly confluent</td>
<td>Not confluent at each axis-junctions</td>
<td>Not confluent at each axis-junctions</td>
<td>Not confluent at each axis-junctions</td>
<td>Not confluent at each axis-junctions</td>
<td>Not confluent at each axis-junctions</td>
</tr>
<tr>
<td><strong>Grooves on the adaxial surfaces of rachis, costae and costules</strong></td>
<td>Orbicular; subterminal on veinlets</td>
<td>Orbicular; subterminal on veinlets</td>
<td>Semi-globose; dorsal on veinlets</td>
<td>Semi-globose; subterminal on veinlets</td>
<td>Globose; dorsal on medium or basal portion of veinlets</td>
<td>Globose, with long thin stalk; dorsal on veinlets</td>
</tr>
<tr>
<td><strong>Sori</strong></td>
<td>Orbicular-reiniform, superior, attached by sinus, entire; rarely exindusiate</td>
<td>Orbicular-reiniform, superior, attached by sinus, entire or eroded</td>
<td>Spathulate-ligulate to nearly orbicular, lateral, attached by a gradually narrowed base on the elevated receptacles under the sori</td>
<td>Semi-circular or cup-shaped, inferior, attached by broad base, enclosing sori when young; receptacle elevated</td>
<td>Globose, inferior, attached by broad base, enclosing sori when young, 2 or 3 valves from top when mature</td>
<td>Globose, inferior, terminal on thin stalk, enveloping sori when young, 2 or 3 valves from top when mature</td>
</tr>
<tr>
<td><strong>Perispore</strong></td>
<td>Bearing reticulate folds</td>
<td>Bearing non-reticulate folds</td>
<td>Bearing reticulate folds</td>
<td>Bearing reticulate folds</td>
<td>Bearing reticulate folds</td>
<td>Bearing reticulate folds</td>
</tr>
</tbody>
</table>
Systematic Botany

D. maximowicziana (Miq.) C. Chr. subsp. scabrosa (Miq.) C. Chr.

Distribution—This species is mainly distributed in India (Assam), Nepal, Papua New Guinea, and the Philippines (Luzon).


Distribution—This species has a restricted distribution in S and SW China, Japan, and Taiwan.


Distribution—This species is endemic to Sri Lanka.


Distribution—This species is endemic to S India.


Polypodium nigrescens Bedd., Ferns S. India t. 169. 1864, non Blume 1828.
Distribution—This species is endemic to S India.


Distribution—This species is endemic to SW China.


Diagnosis—Somewhat resembling Dryopteris subg. Notohperanema sect. Diacalpe, but differing by its indusia. Sect. Stenolepia has spathulate-ligulate to nearly orbicular, and laterally attached indusia, while sect. Diacalpe has glbose and inferior indusia (Table 2).

Morphology—Small to somewhat large terrestrial ferns. Rhizomes scaly, ascending to erect. Fronds clustered; stipes densely covered by broad lanceolate scales but gradually thinning to smaller, lanceolate, linear or filiform trichomes distally; larger scales often inserted on dark warts and thus the leaf axes usually dark-verrucate; laminae decompound, usually tri- to quadripinnate, rarely pentapinnatifid in larger individuals; the dromy (dissection pattern) of pinnae puci-dromous (viz. anadromy, catadromy or even isodromy could be found in all pinnae of the same frond; cf. Kramer 1987); adaxial surface of rachises, costae and costules grooved but thinning to smaller, lanceolate, linear or filiform trichomes (Fig. 1D), but much more plentiful on the adaxial sides; short, conical, reddish-brown setae present on the adaxial side of junctions of veins; small oval glandular hairs present or absent — if present, persistent on abaxial surface of costae and veins; terminal segments of lateral pinnae usually obtuse to subacute, sinuate to pinnatifid. Venation abaxially dark, clearly visible; veins free, pinnately branching, simple or once to twice forked, veinlet tips almost reaching the margin. Sori semi-globose, dorsal on a vein or veinlet or at the forking of a vein; receptacles elevated; indusium is attached by a gradually narrowed base on the elevated receptacle under the sorus, spathulate-ligulate to approximately orbicular, usually fugacious. Spores bilateral, monolete, ellipsoid, the surface with prominent, coarse folds.

Distribution Range—This species occurs in central, eastern and northern Malesia [incl. Borneo, Indonesia, New Guinea (incl. Papua New Guinea), and the Philippines] (cf. Kramer et al. 1990; Chang et al. 2013). Hence, intensive sampling from the whole range of the species is necessary for further phylogenetic analyses.

Included Species—Only one species, Dryopteris hypolepioides Rosenst., is recognized currently. However, two uncertain taxa documented in Johns et al. (2006) are also listed below.


Lastraea tristis (Blume) T. Moore, Index Fil. 107. 1858.


Distribution—It is the same as the distribution range of this section.

Uncertain Taxa—


Distribution—This taxon is currently only known from Indonesia (Prov. Papua; type locality).


Distribution—This taxon is currently only known from Indonesia (Prov. Papua).

Key to Sections of Subg. Notohperanema

1. Indusia superior (above sori), flat, reniform; scales on stipes, at least the basal portion, often patent or not .......................... 2
2. Scales on stipes and rachises lanceolate to ovate-lanceolate, patent on basal portion of stipes or not; grooves of rachis, costae and costules not confluent at junctions (Fig. 1C) .......................................................... sect. Stenolepia

sect. Notohperanema

Dryopteris, the new combination based on A. triste Blume was blocked by D. tristis (Kunze) Kuntze (Revis. Gen. Pl. 2: 814. 1891). Thus, D. hypolepioides Rosenst. (Reptert. Spec. Nov. Regni Veg. 12: 175. 1913), which is one of the two earliest published taxa and recently regarded as a synonym of A. triste (Chang et al. 2013), was chosen to be the replacement name. However, judging from the somewhat variable characters, such as plant size (from 13 cm to 100 cm tall), lamina shape (from subtriangular-triangular to ovate-lanceolate), lamina dissection (ranging from tripinnatifoliate to pentapinnatifid), shape and texture of indusia (broad-ovate to orbicular with membraneous texture for the Philippine materials vs. small, narrow, spathulate-ligulate with rigid texture according to the description of type protolog), occurrence of glandular hairs on abaxial surface of fronds (cf. Johns et al. 2006), types of substrate on which they grow (from loam to limestone), and habitat ecology (from the grounds under the forest canopies at middle elevations to the exposed summit areas at high altitudes), some cryptic species might possibly be included therein. Hence, intensive sampling from the whole range of the species is necessary for further phylogenetic analyses.

Included Species—Only one species, Dryopteris hypolepioides Rosenst., is recognized currently. However, two uncertain taxa documented in Johns et al. (2006) are also listed below.

1. Indusia lateral (spathulate-ligulate to approximately orbicular) or inferior (beneath sori; globose or semi-globose); scales on stipes and rachises appressed, ascending or sometimes reflexed, except sect. Peranema .......................................................... 3

2. Indusia lateral (attached by a gradually narrowed base on the elevated receptacle under sori), spathulate-ligulate to approximately orbicular, often fugacious; scales on stipes mostly appressed ........................................... sect. Stenolepia

3. Indusia inferior (beneath sori), globose or semi-globose; the positions of scales on stipes relative to stipe surface in various ways ........................................................................................................... 4

4. Sori stalked; indusia globose (Fig. 1F); scales on stipes and rachises mostly patent .............................................................. sect. Peranema

5. Sori sessile; indusia globose or semi-globose; scales on stipes and rachises appressed, ascending or sometimes reflexed .............................................................. sect. Acrophorus

5. A large, membranaceous, cordate or ovate-lanceolate, often persistent scale usually present at each junction of pinna and pinnule on abaxial surface (Fig. 1B); indusia memranaceous, semi-globose ........................................ sect. Acrophorus

5. Leaf axes of every order without a large cordate or ovate-lanceolate scale; indusia leathery, globose (Fig. 1E) ........................................................................ sect. Diacalpe

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Literature Cited


Appendix 1. Voucher specimens and GenBank accession numbers for cpDNA sequences used in this study. Information is presented in the following order: taxon name, collection number (deposited herbarium), locality, chlL, ndhF, matK, rps16-matK IGS, trnl-F.

Appendix 2. The materials used in perispore morphology examination.