



## On the monophyly of subfamily Tectarioideae (Polypodiaceae) and the phylogenetic placement of some associated fern genera

FA-GUO WANG<sup>1</sup>, SAM BARRATT<sup>2</sup>, WILFREDO FALCÓN<sup>3</sup>, MICHAEL F. FAY<sup>4</sup>, SAMULI LEHTONEN<sup>5</sup>, HANNA TUOMISTO<sup>5</sup>, FU-WU XING<sup>1</sup> & MAARTEN J. M. CHRISTENHUSZ<sup>4</sup>

<sup>1</sup>Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China. E-mail: wangfg@scib.ac.cn

<sup>2</sup>School of Biological and Biomedical Science, Durham University, Stockton Road, Durham, DH1 3LE, United Kingdom.

<sup>3</sup>Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8075 Zurich, Switzerland.

<sup>4</sup>Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 4DS, United Kingdom. E-mail: m.christenhusz@kew.org (author for correspondence)

<sup>5</sup>Department of Biology, University of Turku, FI-20014 Turku, Finland.

### Abstract

The fern genus *Tectaria* has generally been placed in the family Tectariaceae or in subfamily Tectarioideae (placed in Dennstaedtiaceae, Dryopteridaceae or Polypodiaceae), both of which have been variously circumscribed in the past. Here we study for the first time the phylogenetic relationships of the associated genera *Hypoderris* (endemic to the Caribbean), *Cionidium* (endemic to New Caledonia) and *Pseudotectaria* (endemic to Madagascar and Comoros) using DNA sequence data. Based on a broad sampling of 72 species of eupolypods I (= Polypodiaceae *sensu lato*) and three plastid DNA regions (*atpA*, *rbcL* and the *trnL-F* intergenic spacer) we were able to place the three previously unsampled genera. Our results show that *Cionidium*, like *Ctenitopsis*, *Fadyenia*, *Hemigramma* and *Quercifilix*, is embedded in *Tectaria*, and the monophyly of *Tectaria* is therefore corroborated only if these segregate genera are included. *Hypoderris* is sister to *Tectaria brauniana* and together they are sister to *Triplophyllum*, which was found to be monophyletic. Despite their morphological similarity with *Tectaria*, the genera *Pleocnemia* and *Pseudotectaria* were placed in Dryopteridoideae. Polypodiaceae subfamily Tectarioideae (former family Tectariaceae) is hereby defined to include *Arthropteris*, *Hypoderris*, *Pteridrys*, *Tectaria* and *Triplophyllum*. *Aenigmopteris* may also belong here, but this genus remains unsampled.

**Key words:** *Cionidium*, Dryopteridaceae, eupolypods I, *Hypoderris*, leptosporangiate ferns, neoteny, paedomorphism, *Pseudotectaria*, *Tectaria brauniana*, Tectariaceae, *Triplophyllum*

### Introduction

The fern genus *Tectaria* Cav. is currently considered a part of Tectariaceae (*sensu* Smith *et al.* 2006, Christenhusz *et al.* 2011) or Polypodiaceae subfamily Tectarioideae (*sensu* Christenhusz & Chase 2014), the classification followed in this paper. Tectarioideae is a medium-sized group of ferns with a pantropical distribution. The species have diverse morphologies, especially in characters such as leaf shape, venation, soral organisation, indumentum and variability in indusia, and several species show leaf dimorphism. Ever since Tectariaceae was first described as a family by Ching (1940), there has been taxonomic controversy on its circumscription and placement.

Most authors have included between 15 and 25 genera in the loosely defined lineage containing *Tectaria* (e.g. Ching 1940, 1978, Holttum 1947), but the identities of these genera have varied greatly. In Holttum's (1947) classification, the group was placed in Dennstaedtiaceae as subfamily Tectarioideae. It included the genera *Amphiblestra* C.Presl, *Arcypteris* Underw., *Ctenitis* (C.Chr.) C.Chr., *Cyclopeltis* J.Sm., *Dictyoxiphium* Hook., *Hemigramma* Christ, *Heterogonium* C.Presl, *Lastreopsis* Ching, *Pleocnemia* C.Presl, *Pleuroderris* Maxon,

## References

- Asama, K. (1960) Evolution of the leaf forms through the ages explained by the successive retardation and neoteny. Part 1, outline of retardation. *Science Reports of the Tohoku University, 2nd series, Geology. special volume 4*: 252–280.
- Bower, F.O. (1928) *The ferns (Filicales). Vol. III. The leptosporangiate ferns*. Cambridge University Press, Cambridge.
- Buerki, S., Forest, F., Acevedo-Rodríguez, P., Callmander, M.W., Nylander, J.A.A., Harrington, M., Sanmartín, I., Küpfer, P. & Alvarez, P. (2009) Plastid and nuclear DNA markers reveal intricate relationships at subfamilial and tribal levels in the soapberry family (Sapindaceae). *Molecular Phylogenetics and Evolution* 51: 238–258.  
<http://dx.doi.org/10.1016/j.ympev.2009.01.012>
- Cavanilles, A.J. (1802) *Descripción de las plantas*. Imprenta Real, Madrid.
- Chase, M.W. & Hills, H.H. (1991) Silica gel: an ideal material for field preservation of leaf samples for DNA studies. *Taxon* 40: 215–220.  
<http://dx.doi.org/10.2307/1222975>
- Ching, R.-C. (1931) The studies of Chinese ferns VII. A revision of the genus *Tectaria* from China and Sikkime-Himalaya. *Sinensia* 2: 9–36.
- Ching, R.-C. (1940) On natural classification of the family “Polypodiaceae”. *Sunyatsenia* 5: 201–268.
- Ching, R.-C. (1978) The Chinese fern families and genera: systematic arrangement and historical origin. *Acta Phytotaxonomica Sinica* 16(3): 1–19; 16(4): 16–37.
- Christ, H. (1906) Filices guatemalenses. *Bulletin de l'Herbier Boissier, sér. 2* 6: 289–293.
- Christenhusz, M.J.M. (2007) *Dracoglossum*, a new Neotropical fern genus (Pteridophyta). *Thaiszia, Journal of Botany* 17: 1–10.
- Christenhusz, M.J.M. (2010a) *Danaea* (Marattiaceae) revisited: biodiversity, a new classification and ten new species of a neotropical fern genus. *Botanical Journal of the Linnean Society* 163: 360–385.  
<http://dx.doi.org/10.1111/j.1095-8339.2010.01061.x>
- Christenhusz, M.J.M. (2010b) New combinations in the fern genus *Tectaria* (Tectariaceae) for the *Flora of China*. *Phytotaxa* 10: 58–59.
- Christenhusz, M.J.M. & Chase, M.W. (2013) Biogeographical patterns of plants in the Neotropics – dispersal rather than plate tectonics is most explanatory. *Botanical Journal of the Linnean Society* 171: 277–286.  
<http://dx.doi.org/10.1111/j.1095-8339.2012.01301.x>
- Christenhusz, M.J.M. & Chase, M.W. (2014) Trends and concepts in fern classification. *Annals of Botany* 113: 571–594.
- Christenhusz, M.J.M., Jones, M., Lehtonen, S. (2013) Phylogenetic placement of the enigmatic fern genus *Dracoglossum*. *American Fern Journal* 103: 131–138.
- Christenhusz, M.J.M., Tuomisto, H., Metzgar, J.S., Pryer, K.M. (2008) Evolutionary relationships within the Neotropical eusporangiate fern genus *Danaea*. *Molecular Phylogenetics and Evolution* 46: 34–48.  
<http://dx.doi.org/10.1016/j.ympev.2007.09.015>
- Christenhusz, M.J.M., Zhang X.-C. & Schneider, H. (2011) A linear sequence of extant families and genera of lycophytes and ferns. *Phytotaxa* 19: 7–54.
- Christensen, C. (1913) A monograph of the genus *Dryopteris* part I. The tropical American pinnatifid-bipinnatifid species. *Kongelige Danske Videnskabernes Selskab Skrifter. Naturvidenskabelige og Mathematiske Afdeling* 7: 55–282
- Christensen, C. (1931) Asiatic pteridophyta collected by Joseph F. Rock 1920–1924. *Contributions from the United States National Herbarium* 26: 265–338.
- Christensen, C. (1934) *Index filicum: supplementum tertium pro annis 1917–1933*. Hagerup, Copenhagen.
- Copeland, E.B. (1907) A revision of *Tectaria* with special regard to the Philippine species. *Philippine Journal of Science* 2: 409–418.
- Copeland, E.B. (1917) Keys to the ferns of Borneo. *Sarawak Museum Journal* 2: 288–424.
- Copeland, E.B. (1928) *Leptochilus* and genera confused with it. *Philippine Journal of Science* 37: 333–416.
- Copeland, E.B. (1929) Pteridophyta Novae Caledoniae. *University of California Publications in Botany* 14: 353–369.
- Copeland, E.B. (1947) *Genera filicum, the genera of ferns*. Waltham: Chronica Botanica.
- Ding, H.-H., Chao, Y.-S. & Dong, S.-Y. (2013) Taxonomic novelties in the fern genus *Tectaria* (Tectariaceae). *Phytotaxa* 122: 61–64.
- Doyle, J.J. & Doyle, J.L. (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin of the Botanical Society of America* 19: 11–15.
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.  
<http://dx.doi.org/10.1093/nar/gkh340>
- Edwards, P.J. (1991) Variation in *Fadyenia hookeri*. *Curtis's Botanical Magazine* 8: 140–146.  
<http://dx.doi.org/10.1111/j.1467-8748.1991.tb00376.x>
- Fournier, E.P.N. (1872) *Sertum nicaraguense*. *Bulletin de la Société Botanique de France* 19: 247–263.
- Gómez P., L.D. & Gómez-L., J. (1982) *Plantae mesoamericanae novae. V. Phytologia* 51: 474–478.
- Gordon, D.R. & Thomas, K.P. (1997) *Strangers in paradise, impact and management of nonindigenous species in Florida*. Island Press, Washington.

- Hall, T.A. (1999) Bio-Edit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hasebe, M., Wolf, P.G., Pryer, K.M., Ueda, K., Ito, M., Sano, R., Gastony, G.J., Yokoyama, J., Manhart, J.R., Murakami, M., Crane, E.H., Haufler, C.H. & Hauk, W.D. (1995) Fern phylogeny based on *rbcL* nucleotide sequences. *American Fern Journal* 85: 134–181.  
<http://dx.doi.org/10.2307/1547807>
- Henfrey, A., Moore, T. & Ayres, W.P. (1852) *Garden companion and florists' guide*. Orr, London.
- Hieronymus, G. (1907) *Plantae Stuebelianae, Pteridophyta. Zweiter Teil. Hedwigia* 46: 322–336.
- Holttum, R.E. (1947) A revised classification of leptosporangiate ferns. *Journal of the Linnean Society, Botany* 53: 123–158.  
<http://dx.doi.org/10.1111/j.1095-8339.1947.tb02554.x>
- Holttum, R. E. (1951a) The fern-genus *Pleocnemia* Pr. *Reinwardtia* 1: 171–189.
- Holttum, R. E. (1951b) The fern-genus *Arcypteris* Underwood (*Dictyopteris* Presl *sensu* Fée). *Reinwardtia* 1: 191–196.
- Holttum, R.E. (1983) The fern-genera *Tectaria*, *Heterogonium* and *Ctenitis* in the Mascarene Islands. *Kew Bulletin* 38: 107–130.  
<http://dx.doi.org/10.2307/4107974>
- Holttum, R.E. (1986) Studies in the fern-genera allied to *Tectaria* V. *Triplophyllum*, a new genus of Africa and America. *Kew Bulletin* 41: 237–260.  
<http://dx.doi.org/10.2307/4102928>
- Holttum, R.E. (1987) Studies in the fern genera allied to *Tectaria* Cav. VI. A conspectus of genera in the Old World regarded as related to *Tectaria*, with description of two new genera. *Garden's Bulletin of the Straights Settlement* 39: 153–167.
- Holttum, R.E. (1988) Studies in the fern genera allied to *Tectaria* Cav. VII. Species of *Tectaria* sect. *Sagenia* (Presl) Holttum in Asia excluding Malesia. *Kew Bulletin* 43: 475–489.  
<http://dx.doi.org/10.2307/4118979>
- Holttum, R.E. & Edwards, P.J. (1986) Studies in the fern-genera allied to *Tectaria* II. *Dryopsis*, a new genus. *Kew Bulletin* 41: 171–204.
- Holttum, R.E. & Lin, Y.X. (1990) A re-assessment of the fern genus *Pseudotectaria*. *Kew Bulletin* 45: 257–263.  
<http://dx.doi.org/10.2307/4115683>
- Hooker, W.J. (1838–1842) *Genera Filicum*. Bohn, London.
- Hooker, W.J. (1844) Dicksonieae, *Species Filicum* 1: 14–58.
- Hooker, W.J. & Bauer, F. (1840) *Genera Filicum; or illustrations of the genera of ferns*. Bohn, London.
- Karsten, H. (1859) *Florae Columbiae terrarumque adiacentium specimina selecta, tomus primus*. Dümmler, Berlin.  
<http://dx.doi.org/10.5962/bhl.title.400>
- Kramer, K.U., Holttum, R.E., Moran, R.C. & Smith, A.R. (1990) Dryopteridaceae. pp. 101–144, in: Kubitzki, K. (ed.) *The families and genera of vascular plants. Vol 1. Pteridophytes and gymnosperms*. Springer, Berlin.  
[http://dx.doi.org/10.1007/978-3-662-02604-5\\_23](http://dx.doi.org/10.1007/978-3-662-02604-5_23)
- Kuo, C.-M. (2002) Nomenclature changes for some pteridophytes of Taiwan. *Taiwania* 47: 170–174.
- Kuo, L.-Y., Li, F.-W., Chiou, W.-L. & Wang, C.-N. (2011) First insights into fern *matK* phylogeny. *Molecular Phylogenetics and Evolution* 59: 556–566.  
<http://dx.doi.org/10.1016/j.ympev.2011.03.010>
- Lehtonen, S. (2011) Towards resolving the complete fern tree of life. *PLoS ONE* 6(10): e24851.  
<http://dx.doi.org/10.1371/journal.pone.0024851>
- Lellinger, D.B. (1968) Notes on Ryukyu ferns. *American Fern Journal* 58: 155–158.  
<http://dx.doi.org/10.2307/1545950>
- Lellinger, D.B. (2003) Nomenclatural and taxonomic notes on the pteridophytes of Costa Rica, Panama, and Colombia, III. *American Fern Journal* 93: 146–151.
- Li, C.-X. & Lu, S.-G. (2006) Phylogenetic analysis of Dryopteridaceae based on chloroplast *rbcL* sequences. *Acta Phytotaxonomica Sinica* 44(5): 503–515.  
<http://dx.doi.org/10.1360/aps050081>
- Liu, H.-M., Zhang, X.-C. & Chen, Z.-D. (2007) Polyphyly of the fern family Tectariaceae *sensu* Ching: insights from cpDNA sequence data. *Science in China C, Life Sciences* 50(6): 789–798.  
<http://dx.doi.org/10.1007/s11427-007-0099-9>
- Liu, H.-M., Jiang, R.-H., Guo, J., Hovenkamp, P., Perrie, L. R., Shepherd, L., Hennequin, S. & Schneider, H. (2013) Towards a phylogenetic classification of the climbing fern genus *Arthropteris*. *Taxon* 62: 688–700.  
<http://dx.doi.org/10.12705/624.26>
- Liu, H.-M., He, L.-J., Schneider, H. (2014) Towards the natural classification of tectarioid ferns: Confirming the phylogenetic relationships of *Pleocnemia* and *Pteridrys* (eupolypods I). *Journal of Systematics and Evolution*.  
<http://dx.doi.org/10.1111/jse.12073>
- Maxon, W.R. (1926) Pteridophyta of Porto Rico and the Virgin Islands. *Scientific Survey of Porto Rico and the Virgin Islands* 6: 461–483.
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme van Reine, W.F., Smith, G.F., Wiersema J.H. & Turland, N.J. (2012) *International code of*

*nomenclature for algae, fungi, and plants (Melbourne Code), adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Regnum Vegetabile 154. Koeltz, Koenigstein.*

- Moran, R.C. & Smith, A.R. (2001) Phytogeographic relationships between neotropical and African-Madagascan pteridophytes. *Brittonia* 53: 304–351.  
<http://dx.doi.org/10.1007/bf02812704>
- Moran, R.C., Labiak, P. & Sundue, M. (2010) Synopsis of *Mickelia*, a newly recognized genus of bolbitidoid ferns (Dryopteridaceae). *Brittonia* 62: 337–356.  
<http://dx.doi.org/10.1007/s12228-010-9158-9>
- Muellner, A.N., Samuel, R., Chase, M.W., Pannell, C.M. & Greger, H. (2005) *Aglaia* (Meliaceae): an evaluation of taxonomic concepts based on DNA data and secondary metabolites. *American Journal of Botany* 92: 534–543.  
<http://dx.doi.org/10.3732/ajb.92.3.534>
- Nylander, J.A.A. (2004) MrModeltest, version 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University. <http://www.abc.se/~nylander/mrmodeltest2/mrmodeltest2.html>
- Pichi-Sermolli, R.E.G. (1977) Tentamen pteridophytorum genera in taxonomicum ordinem redigendi. *Webbia* 31: 313–512.  
<http://dx.doi.org/10.1080/00837792.1977.10670077>
- Pichi-Sermolli, R.E.G. (1991) On the taxonomy and nomenclature of some species from tropical Africa of the genus *Triplophyllum* Holttum (Dryopteridaceae). *Webbia* 45: 117–135.  
<http://dx.doi.org/10.1080/00837792.1991.10670493>
- Prado, J. & Moran, R.C. (2008) Revision of the neotropical species of *Triplophyllum* (Tectariaceae). *Brittonia* 60: 103–130.  
<http://dx.doi.org/10.1007/s12228-008-9024-1>
- Prentice, C. (1896) On a new species of *Hypoderris*. *Journal of Botany, British and Foreign* 7: 240.
- Pryer, K.M. & Hearn, D.J. (2009) Evolution of leaf form in marsileaceous ferns: evidence for heterochrony. *Evolution* 63: 498–513.  
<http://dx.doi.org/10.1111/j.1558-5646.2008.00562.x>
- Pryer, K.M., Smith, A.R., Hunt, J.S. & Dubuisson, J.-Y. (2001) *RbcL* data reveal two monophyletic groups of filmy ferns (Filicopsida: Hymenophyllaceae). *American Journal of Botany* 88: 1118–1130.  
<http://dx.doi.org/10.2307/2657095>
- Pryer, K.M., Schuettpelz, E., Wolf, P.G., Schneider, H., Smith, A.R. & Cranfill, R. (2004) Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. *American Journal of Botany* 91: 1582–1598.  
<http://dx.doi.org/10.3732/ajb.91.10.1582>
- Renner, S.S. (1999) Circumscription and phylogeny of the Laurales: evidence from molecular and morphological data. *American Journal of Botany* 86: 1301–1315.  
<http://dx.doi.org/10.2307/2656778>
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.  
<http://dx.doi.org/10.1093/bioinformatics/btg180>
- Saghai-Marouf, M.A., Soliman, K.M., Jorgensen, R.A. & Allard, R.W. (1984) Ribosomal DNA spacer-length polymorphisms in barley: Mendelian inheritance, chromosomal location, and population dynamics. *Proceedings of the National Academy of Sciences of the USA* 81: 8014–8018.  
<http://dx.doi.org/10.1073/pnas.81.24.8014>
- Schuettpelz, E., Korall, P. & Pryer, K.M. (2006) Plastid *atpA* data provide improved support for deep relationships among ferns. *Taxon* 55: 897–906.  
<http://dx.doi.org/10.2307/25065684>
- Schuettpelz, E. & Pryer, K.M. (2007) Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. *Taxon* 56: 1037–1050.  
<http://dx.doi.org/10.2307/25065903>
- Sledge, W.A. (1972) The tectarioid ferns of Ceylon. *Kew Bulletin* 27: 407–424.  
<http://dx.doi.org/10.2307/4114354>
- Smith, A.R. (1995) Non-molecular phylogenetic hypotheses for ferns. *American Fern Journal* 85: 104–122.  
<http://dx.doi.org/10.2307/1547805>
- Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G. (2006) A classification of extant ferns. *Taxon* 55: 705–731.  
<http://dx.doi.org/10.2307/25065646>
- Stidd, B.M. (1974) Evolutionary trends in Marattiales. *Annals of the Missouri Botanical Garden* 61: 388–407.  
<http://dx.doi.org/10.2307/2395065>
- Swartz, O. (1801) Genera et species filicum, etc. *Journal für die Botanik [ed. Schrader, H.A.]* 1800: 1–120.
- Swofford, D.L. (2003) *PAUP\* 40: Phylogenetic analysis using parsimony (\*and other methods)*, version 4.0b10. Sinauer, Sunderland.
- Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.  
<http://dx.doi.org/10.1007/bf00037152>

- Tardieu-Blot, M.L. (1955) Sur les Tectarioideae de Madagascar et des Mascareignes avec description d'un genre nouveau *Pseudotectaria*. *Notulae Systematicae* 15: 86–90.
- Tardieu-Blot, M.L. & Christensen, C. (1938) Les fougères d'Indochine XIV. Dryopteridaceae. *Notulae Systematicae* 7: 56–104.
- Tryon, A.F. & Lugardon, B. (1991) *Spores of the Pteridophyta*. Springer, New York.  
<http://dx.doi.org/10.1002/fedr.4910950403>
- Tryon, R.M. & Tryon, A.F. (1981) Taxonomic and nomenclatural notes on ferns. *Rhodora* 83: 133–137.
- Tryon, R.M. & Tryon, A.F. (1982) *Ferns and allied plants, with special reference to tropical America*. Springer, New York.
- Tuomisto, H. & Poulsen, A.D. (1996) Influence of edaphic specialization on pteridophyte distribution in neotropical rain forests. *Journal of Biogeography* 23: 283–293.  
<http://dx.doi.org/10.1046/j.1365-2699.1996.00044.x>
- Underwood, L.M. (1906) American ferns-VI. Species added to the flora of the United States from 1900 to 1905. *Bulletin of the Torrey Botanical Club* 33: 189–205.
- Wagner, W.H.Jr., Wagner, F.S. & Gomez P, L.D. (1978) The singular origin of a Central American fern, *Pleuroderris michleriana*. *Biotropica* 10: 254–264.  
<http://dx.doi.org/10.2307/2387677>
- Wolf, P.G., Soltis, P.S. & Soltis, D.E. (1994) Phylogenetic relationships of dennstaedtioid ferns: evidence from *rbcL* sequences. *Molecular Phylogenetics and Evolution* 3: 383–392.  
<http://dx.doi.org/10.1006/mpev.1994.1044>
- Xing, F., Yan, Y., Dong, S., Wang, F., Christenhusz, M.J.M. & Hovenkamp, P. (2013) Tectariaceae, in: Wu, Z., Raven, P.H. & Hong, D. (ed.) *Flora of China, vol. 2–3, Lycopodiaceae through Polypodiaceae*. Science Press, Beijing, pp. 730–746.
- Zhang, L.-B. (2012) Reducing the fern genus *Dryopsis* to *Dryopteris* and the systematics and nomenclature of *Dryopteris* subgenus *Erythrovariae* section *Dryopsis* (Dryopteridaceae). *Phytotaxa* 71: 17–27.