Article

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

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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,

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Pteridrys C.Chr. & Ching, *Quercifilix* Copel., *Stenosemia* C.Presl and *Tectaria*. Several genera, including *Chlamydogramme* Holttum (1987), *Dryopsis* Holttum & Edwards (1986), *Megalastrum* Holttum (1987), *Pseudotectaria* Tardieu-Blot (1955) and *Triplophyllum* Holttum (1986), were added to this in later studies. The same assembly of genera was treated as a subfamily of Dryopteridaceae rather than Dennstaedtiaceae (e.g. Kramer *et al.* 1990), when morphological data had shown that the lineage appeared more similar to the dryopterids rather than the dennstaedtioids.

With the advent of molecular research from the mid-1990s, the lineages of leptosporangiate ferns were recircumscribed (see Christenhusz & Chase 2014). Hasebe *et al.* (1995) already found *Tectaria* to be more closely related to *Oleandra* than to Dryopteridaceae with which it was usually associated. Further studies have supported this position, which culminated in the recircumscription of Tectariaceae based on a combination of morphological and molecular data (e.g. Smith *et al.* 2006, Christenhusz *et al.* 2011). In these classifications, several genera were synonymised with *Tectaria* (*Amphiblestra*, *Bathmium* C.Presl ex Link, *Camptodium* Fée, *Cardiochlaena* Fée, *Chlamydogramme*, *Cionidium* T.Moore, *Ctenitopsis* Ching ex Tardieu & C.Chr., *Dictyoxiphium*, *Dryomenis* Fée ex J.Sm., *Fadyenia* Hook., *Grammatosorus* Regel, *Hemigramma*, *Heterogonium*, *Lenda* Koidz., *Luerssenia* Kuhn ex Luerssen, *Microbrochis* C.Presl, *Phlebiogonium* Fée, *Pleuroderris*, *Podopeltis* Fée, *Pseudotectaria*, *Quercifilix*, *Sagenia* C.Presl and *Stenosemia*). In addition to *Tectaria* itself, Tectariaceae included the genera *Aenigmopteris* Holttum, *Arthropteris* J.Sm. ex Hook.f., *Hypoderris* R.Br. ex Hook., *Pleocnemia*, *Psammiosorus* C.Chr., *Psomiocarpa* C.Presl, *Pteridrys* and *Triplophyllum*. At the same time, it was concluded that Tectariaceae *sensu* Holttum (1947) is polyphyletic. In order to obtain a monophyletic Tectariaceae, some genera previously considered to be 'tectarioid' were moved to Dryopteridaceae (*Ctenitis*, *Dryopsis* and *Lastreopsis*; Smith *et al.* 2006, Li & Lu 2006, Liu *et al.* 2007, Christenhusz *et al.* 2011) and others to Lomariopsidaceae (*Cyclopeltis*; Smith *et al.* 2006, Schuettpelz & Pryer 2007). *Dracoglossum* Christenh., which was segregated from *Tectaria* on the basis of habit and spore characters (Christenhusz 2007), has since been found to be sister to *Cyclopeltis* in Lomariopsidaceae (Christenhusz *et al.* 2013) or Polypodiaceae subfamily Lomariopsidoideae (Christenhusz & Chase 2014), depending on the preferred family-level classification.

Holttum (1951a, 1951b) recognized *Pleocnemia* and *Arcypteris* as separate but closely allied genera, but later he synonymised the latter under *Pleocnemia*, an interpretation accepted by Christenhusz *et al.* (2011). The family placement of *Pleocnemia* has been ambiguous. Tryon & Lugardon (1991) included it in Dryopteridaceae, but also suggested on the basis of spore diversity that this family is not a homogeneous group. Smith *et al.* (2006) tentatively placed *Pleocnemia* in Tectariaceae. This was erroneously accepted by Christenhusz *et al.* (2011), but Kuo *et al.* (2011) and Lehtonen (2011) suggested *Pleocnemia* to be part of Dryopteridaceae on the basis of molecular data, which is confirmed by Liu *et al.* (2014), in which *Pleocnemia* was found to be closely related to the bolbitidoid and lastreopsidoid ferns. Even though *Pteridrys* shares the peculiar sinusoid teeth with *Pleocnemia* (resulting in their assumed relationship), the genus *Pteridrys* has always been associated with the tectarioid lineage, a placement that was confirmed by Lehtonen (2011) and Liu *et al.* (2014). The sinusoid teeth are a case of parallel evolution (Liu *et al.* 2014).

Based on sequences from six plastid regions, Liu *et al.* (2013) synonymised the genus *Psammiosorus* with *Arthropteris* and segregated this clade from Tectariaceae as the new family Arthropteridaceae. The monotypic genus *Psomiocarpa* was found to be part of *Tectaria* in an unpublished phylogenetic analysis and its only species was therefore transferred to *Tectaria* as *T. psomiocarpa* S.Y.Dong (in Ding *et al.* 2013).

These recent classifications based on molecular phylogenetic studies have provided new insights into the relationships of genera associated with *Tectaria*. They have also led to repeated shuffling of genera among families and a proliferation of monogeneric families. To provide a stable classification at the family level, Christenhusz & Chase (2014) proposed to unite all families of "eupolypods I" (*sensu* Smith *et al.* 2006) as the single family Polypodiaceae, and to recognise the clades within it at the subfamilial rank. Their Polypodiaceae subfamily Tectarioideae consists of the genera *Aenigmopteris*, *Arthropteris*, *Hypoderris*, *Pteridrys*, *Tectaria* and *Triplophyllum*. This leaves a few genera unplaced, such as *Cionidium* and *Pseudotectaria*. Some of the genera previously placed in Tectariaceae have also been poorly or not at all sampled in earlier phylogenetic studies, such as *Hypoderris* and *Triplophyllum*. In this study we therefore focus on the placement of these genera. We also aim to test the monophyly of Tectarioideae *sensu* Christenhusz & Chase (2014).

Focal genera

Cionidium is a monospecific genus and the single species is endemic to New Caledonia. *Cionidium moorei* T.Moore (in Henfrey et al. 1852: 143) is morphologically similar to many Palaeotropical *Tectaria* species, but its sori are arranged on the leaf margin and placed on stalked receptacles. Although its phylogenetic placement has never been confirmed with molecular data, *Cionidium* is usually treated as a synonym of *Tectaria*.

Hypoderris is also based on a single species, *H. brownii* J.Sm. ex Hooker (1839: t. 1), which is endemic to the Caribbean. It is found on limestone boulders in the rainforests of Hispaniola, Puerto Rico, Grenada and Trinidad and Tobago. It has long-creeping rhizomes, dark purple to brownish scales and simple, lobed leaf blades. It is similar to *Tectaria* in leaf shape, venation and rhizome scales, but differs markedly in its indusium. This is inferior in attachment, globose and becomes saucer-shaped enclosing the sporangia, but is later obscured by the developing sporangia. *Hypoderris* was first described by Brown in Hooker (1838) and was placed in Polypodiaceae (Hooker 1844, Maxon 1926, Christensen 1934). Brown thought *Hypoderris* to be close to *Woodsia* R.Br., but he also stated that its leaves have a similar structure to that of some *Polypodium* L. or *Aspidium* Sw. Based on its unique morphological and anatomical characters, including petioles with four vascular strands and the indusia and sori described above, Bower (1928) suggested placing the genus in Woodsieae, which he considered to be part of the dryopterid ferns. Ching (1940) described a new family Hypoderriaceae on the basis of the unique sori, indusia and spore type. However, this is an invalid name because Ching did not provide a Latin diagnosis (McNeill *et al.* 2012, Art. 39.1) and the family was not accepted in later systems (Pichi-Sermolli 1977, Tryon & Tryon 1982, Kramer *et al.* 1990). All of these authors assigned *Hypoderris* to Dryopteridaceae, usually near *Tectaria*. Because of the long association with *Tectaria* and obvious morphological similarities with that genus, Smith *et al.* (2006) and Christenhusz *et al.* (2011) placed *Hypoderris* in Tectariaceae. The other species having combinations in *Hypoderris* are not closely related to *H. brownii*. One of them (*H. stuebelii* Hieronymus 1907: 323) is a synonym of *Mickelia oligarchica* (Baker) Moran *et al.* (2010: 350; Dryopteridoideae) and others (*H. adnata* Fournier 1872: 260, *H. heteroneuroides* Christ 1906: 292, *H. marginalis* Fournier 1872: 260, *H. seemannii* Prentice 1896: 240) are *Tectaria × michleriana* (D.C.Eaton) Lellinger (2003: 150), a sterile hybrid between *T. incisa* Cavanilles (1802: 249) and *T. panamensis* (Hook.) Tryon & Tryon (1981: 136), also known as ×*Pleuroderris* Maxon (see Wagner *et al.* 1978).

Pseudotectaria is a poorly known genus restricted to Madagascar and the Comoros and was separated from *Tectaria* because of the peculiar shape and venation of the basal and suprabasal pinnae and its basic chromosome number (*Pseudotectaria*: $x = 41$ vs. *Tectaria*: $x = 40$; Holttum & Lin 1990). After its original description, the genus was either placed in Dryopteridaceae (Pichi-Sermolli 1977) close to *Tectaria*, or it was treated as a synonym of *Tectaria* (e.g. Tryon & Tryon 1982, Smith *et al.* 2006). Kramer *et al.* (1990) listed *Pseudotectaria* under *Tectaria*, but placed a question mark before it without providing any explanation for the question mark.

Triplophyllum was described by Holttum (1986) and typified by the West African *Aspidium protensum* Swartz (1801: 36). This and related species had already been recognized as a distinct group by Christensen (1913). Nearly all the species he included in this genus were previously placed in *Ctenitis*, but they differ in having *Tectaria*-like scales. They differ from *Tectaria* in having a long-creeping rhizome and mostly having broadly deltoid, pentagonal leaves. The genus is more diversified in Africa (ca 15 species) than in America (nine species); *Triplophyllum* species have always been difficult to distinguish, but this has been greatly aided by a recent monograph of the genus for the Neotropics (Prado & Moran 2008). Holttum (1986) additionally stated that none of the African species examined cytologically was diploid, and he postulated that most African species were allotetraploid, i.e. derived from hybridization, but of uncertain parentage. He also suggested that the genus originated in Africa before the separation of that continent from South America. Prado & Moran (2008) stated that because the spore morphology of the Neotropical species is similar to those of the African and Madagascan species, it is not evident that the Neotropical species form a monophyletic clade within the genus.

Material and methods

Taxon sampling

Eighty samples representing 72 species of eupolypod ferns were included in the study. Fresh leaf material was obtained from plants of wild origin in the living collections of the Royal Botanic Gardens, Kew, and DNA was

extracted from the fresh tissue. Leaf material preserved in silica gel following the procedure of Chase & Hills (1995) was collected from wild plants during various expeditions to Latin America (Brazil, Ecuador, Panama), Kenya and China (mainly Hainan). *Hypoderris brownii* and *Tectaria heracleifolia* (Willd.) Underwood (1906: 200) were specifically sampled for this study in Puerto Rico. Additional material was obtained from excellently preserved herbarium specimens deposited in the herbarium of Helsinki University (H). Some additional sequences were obtained from GenBank. Table 1 provides a complete list of the samples used for this study. No samples of *Aenigmopteris* could be obtained for this study.

TABLE 1. List of taxa used in this study with voucher information, country of origin and GenBank accession numbers (*rbcL*, *atpA* and *trnL-F intergenic spacer*, respectively)

Species	Voucher	Country	rbcL	atpA	trnL-F
Arachniodes standishii (T.Moore) Ohwi	*Zhang 3468* (PE)	China	EF540722	—	EF540700
Arthropteris altescandens J.Sm.	*Skottsberg 286* (H)	Juan Fernandez Isl.	KF887154	KF897992	KF897940
Arthropteris monocarpa (Cordem.) C.Chr.	*Kukkonen 12551* (H)	Ethiopia	KF887155	KF897993	KF897941
Arthropteris orientalis (J.F.Gmel.) Posth.	*RBG Kew 1955-26801* (K)	Cameroon	KF887156	KF897994	KF897942
Arthropteris orientalis (J.F.Gmel.) Posth.	*Kamau & Christenhusz 597* (EA, H)	Kenya	KF887157	KF897995	KF897943
Arthropteris palisotii (Desv.) Alston	*Fraser-Jenkins 12239* (H)	Mayotte	KF887158	KF897996	KF897944
Arthropteris palisotii (Desv.) Alston	*Xing & Wang 5487* (K)	China	KF887159	KF897997	KF897945
Arthropteris paucivenia (C.Chr.) H.M.Liu *et al.*	*Rakotondrainibe 6585* (P)	Madagascar	EF463268	EF463864	—
Arthropteris tenella (G.Forst.) J.Sm.	*Coveny 9186* (H)	Australia	KF887160	KF897998	KF897946
Cionidium moorei T.Moore	*Alanko 81-1889* (H)	New Caledonia	KF887162	—	KF955995
Ctenitis decurrentipinnata (Ching) Ching	*Wang 5468* (K)	China	KF887163	KF898000	KF897948
Ctenitis eatonii (Baker) Ching	*764233* (TNS)/*Kuo 441*(?)	Japan/Taiwan	AB575093	JF304011	EF177264
Ctenitis sinii (Ching) Ohwi	*Alanko 81-1796* (H)	cultivated	KF887161	KF897999	KF897947
Ctenitis sinii (Ching) Ohwi	*762651* (TNS)	Japan	AB575098	—	—
Cyclopeltis crenata (Fée) C.Chr.	*JXH 5130* (KUN)/*K016940* (KBCC)	China/Taiwan	DQ508766	JF304016	DQ514488
Didymochlaena truncatula (Sw.) J.Sm.	*RBG Edinburgh 1993-3685* (E)/ *Schuettpelz 267* (DUKE)	cultivated/ Ecuador	DQ508769	JF832112	DQ514491
Dryopteris shikokiana (Makino) C.Chr.	*Zhang 1472* (CDBI)	China	JX648112	—	JX535912
Dryopteris sieboldii (T.Moore) Kunze	*762696* (TNS)	Japan	AB575169	—	AB575169
Hypodematium crenatum (Forssk.) Kuhn	*Schneider s.n.* (GOET)/*Hyashi s.n.* (UC)	cultivated/Japan	EF463205	EF463705	AF425122
Hypodematium fordii (Baker) Ching	*763905* (TNS)	Japan	AB575184	—	—
Hypoderris brauniana (H.Karst.) F.G.Wang & Christenh.	*Tuomisto 11912* (TUR)	Ecuador	KF887171	KF898007	KF897955
Hypoderris brauniana (H.Karst.) F.G.Wang & Christenh.	*Jones 1228* (TUR)	Panama	KF926649	—	—
Hypoderris brownii J.Sm.	*Recart & Falcón 95* (UPRRP)	Puerto Rico	KF887164	KF898001	KF897949
Lithostegia foeniculacea (Hook.) Ching	*Lu 155* (KUN)	China	DQ508782	—	DQ514506
Lomagramma matthewii (Ching) Holttum	*Wuzhi-shan HN202* (PE)/*Wuzhisan 448* (MO)	China	EF463134	—	GU376551
Lomariopsis pollicina (Willemet) Mett.	*Rakotondrainibe 6707* (P)	Comoros	EF463235	EF463776	DQ396588
Megalastrum macrotheca (Fée) A.R.Sm. & R.C.Moran	*Christenhusz 4181* (TUR)	Guadeloupe	EF463211	EF463713	—
Nephrolepis biserrata (Sw.) Schott	*Christenhusz 4865* (BM)	Brazil	HQ157305	HQ157268	HQ157337

TABLE 1 (continued)

Species	Voucher	Country	rbcL	atpA	trnL-F
Olfersia cervina (L.) Kunze	*Christenhusz 4082* (TUR)/*Ponsonby M27* (?)	Guadeloupe/?	EF463213	EF463715	DQ514508
Pleocnemia rufinervis (Hayata) Nakai	*K016926* (KBCC?)	Taiwan?	JF303976	JF304012	—
Pleocnemia winitii Holttum	*Wang 5493* (K)	China	KF887165	KF898002	KF897950
Polystichopsis muscosa (Vahl) Proctor	*Christenhusz 2675* (TUR, UC)	Martinique	JN189559	—	JN189128
Polystichum xiphophyllum (Baker) Diels	*Lu 038* (KUN)	China	DQ508788	—	DQ514519
Pseudotectaria biformis (Mett.) Holttum	*Fraser-Jenkins 12222* (H)	Mayotte	KF887166	KF898003	KF897951
Pseudotectaria decaryana (C.Chr.) Tardieu,	*Fraser-Jenkins 12018* (H)	Madagascar	KF887167	KF898004	KF897952
Pseudotectaria fibrillosa (Baker) Holttum	*Fraser-Jenkins 12012* (H)	Madagascar	KF887168	—	—
Pteridrys cnemidaria (Christ) C.Chr. & Ching	*Wang 5483* (K)	China	KF887169	KF898005	KF897953
Pteridrys lofouensis (Christ) C.Chr. & Ching	*Liu BJ01* (PE)	China	EF460687	—	—
Rumohra adiantiformis (G.Forst.) Ching	*Skog s.n.* (GMU)/*Schuettpelz 299* (DUKE)	cultivated	AY818678	EF463727	AY540044
Stigmatopteris longicaudata (Liebm.) C.Chr.	*Barrington 2099A* (VT)	Costa Rica	EF463222	EF463729	DQ514523
Tectaria acerifolia R.C.Moran	*Jones 990* (TUR)	Panama	KF887170	KF898006	KF897954
Tectaria devexa (Kunze ex Mett) Copel.	*Wang 5504* (K)	China	KF887172	KF898008	KF897956
Tectaria dilacerata (Kunze) Maxon	*Alanko 78-1506* (H)	cultivated	KF887173	KF898009	KF897957
Tectaria fernandensis (Baker) C.Chr.	*Fraser-Jenkins 11304* (H)	Cameroon	KF887174	KF898010	KF897958
Tectaria fuscipes (Wall. ex Bedd.) C.Chr.	*Wang 5492* (K)	China	KF887175	KF898011	KF897959
Tectaria gaudichaudii (Mett.) Maxon	*Selling 3605* (H)	Hawaii	KF887176	KF898012	—
Tectaria gemmifera (Fée) Alston	*Kamau & Christenhusz 601* (EA, K)	Kenya	KF887177	KF898013	KF897960
Tectaria harlandii (Hook.) C.M.Kuo	*Wang 5503* (K)	China	KF887178	KF898014	KF897961
Tectaria harlandii (Hook.) C.M.Kuo	*Wang 5503a* (K)	China	KF887179	KF898015	KF897962
Tectaria heracleifolia (Willd.) Underw.	*Ackerman 4707* (UPRRP)	Puerto Rico	KF887180	KF898016	KF897963
Tectaria heterocarpa (Bedd.) C.V.Morton	*Fraser-Jenkins 1727* (H)	Nepal	KF887181	KF898017	KF897964
Tectaria impressa (Fee) Holttum	*Wang 5488* (K)	China	KF887182	KF898018	KF897965
Tectaria incisa Cav.	*Christenhusz 4828* (TUR)	Brazil	KF887184	KF898020	KF897967
Tectaria incisa Cav.	*RBG Kew, living coll 1984-521* (K)	Florida	KF887183	KF898019	KF897966
Tectaria kusukusensis (Hayata) Lellinger	*Wang 5496* (K)	China	KF887186	KF898022	KF897969
Tectaria kusukusensis (Hayata) Lellinger	*Wang 5501* (K)	China	KF887185	KF898021	KF897968
Tectaria martinicensis (Spreng.) Copel.	*Sorsa 97/1964* (H)	Puerto Rico	KF887187	KF898023	KF897970
Tectaria panamensis (Hook.) R.M.Tryon & A.F.Tryon	*Jones 1052* (TUR)	Panama	KF887188	KF898024	—
Tectaria paradoxa (Fée) Sledge	*RBG Kew 1964-33125* (K)	New Caledonia	KF887189	KF898025	KF897971
Tectaria phaeocaulis (Rosenst.) C.Chr.	*Wang 5481* (K)	China	KF887190	KF898026	KF897972
Tectaria pica (L.f.) C.Chr.	*RBG Kew 2010-1946* (K)	Mauritius	KF887191	KF898027	KF897973
Tectaria prolifera (Hook.) R.M.Tryon & A.F.Tryon	*Alanko 78-893* (H)	cultivated	KF887192	KF898028	KF897974
Tectaria pubens R.C.Moran	*Tuomisto 11766* (TUR)	Ecuador	KF887193	KF898029	KF897975
Tectaria sagenioides (Mett.) Christenh.	*Wang 5502* (K)	China	KF887194	—	KF897976
Tectaria simonsii (Baker) Ching	*Wang 5495* (K)	China	KF887195	KF898030	KF897977
Tectaria singaporiana (Wall.) Copel.	*Christenhusz 6595* (H)	Malaysia	KF887196	KF898031	KF897978

TABLE 1. (Continued)

Species	Voucher	Country	rbcL	atpA	trnL-F
Tectaria subsageniacea (Christ) Christenh.	*Wang 5485* (K)	China	KF887197	KF898032	KF897979
Tectaria subtriphylla (Hook. & Arn.) Copel.	*Wang 5486* (K)	China	KF887198	KF898033	KF897980
Tectaria trifoliata (L.) Cav.	*Sorsa 123/1965* (H)	Puerto Rico	KF887199	—	KF897981
Tectaria variolosa (Wall.) C.Chr.	*Fraser-Jenkins 3910* (H)	India	KF887200	KF898034	KF897982
Tectaria vivipara (Jermy) T.G.Walker	*Tuomisto 15677* (TUR)	Brazil	KF887201	KF898035	KF897983
Tectaria zeilanica (Houtt.) Sledge	*Wang 5451* (K)	China	KF887202	KF898036	KF897984
Triplophyllum crassifolium Holttum	*Tuomisto 15691* (TUR)	Brazil	KF887203	KF898037	KF897985
Triplophyllum dicksonioides (Fée) Holttum	Tuomisto 15222 (TUR)	Brazil	KF887204	KF898038	KF897986
Triplophyllum funestum (Kunze) Holttum	*Tuomisto 15611* (TUR)	Brazil	KF887206	KF898040	KF897988
Triplophyllum funestum (Kunze) Holttum	*Hormia 2092* (H)	Peru	KF887205	KF898039	KF897987
Triplophyllum glabrum J.Prado & R.C.Moran	*Tuomisto 15444* (TUR)	Brazil	KF887207	KF898041	KF897989
Triplophyllum heudelotii Pic.Serm.	*Fraser-Jenkins 11416* (H)	Cameroon	KF887208	KF898042	KF897990
Triplophyllum hirsutum (Holttum) J.Prado & R.C.Moran	*Tuomisto 15438* (TUR)	Brazil	KF887209	KF898043	—
Triplophyllum vogelii (Hook.) Holttum	*Fraser-Jenkins 11424* (H)	Cameroon	KF887210	KF898044	KF897991.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from the available leaf tissue (dried or fresh). Tissue was ground in porcelain mortars with sterilized sea sand. Extractions used a modified 2× CTAB protocol (Doyle & Doyle 1987, Saghai-Maroof *et al.* 1984) as standard for preservation in the Kew DNA bank (see http://apps.kew.org/dnabank/introduction.html), and were further purified using a $CsCl_2$/ethidium bromide density gradient (1.55 g/ml; see Muellner *et al.* 2005) and dialysis. The selected DNA regions were amplified with standard polymerase chain reaction (PCR). We sampled three plastid regions: *atpA*, *rbcL* and the *trnL-F* intergenic spacer (IGS).

The *rbcL* gene was amplified and sequenced using the 26-nucleotide forward primer 1F (5′-ATGTCACCACAAACGGAGACTAAAGC-3′), the 26-nucleotide reverse primer 1361R (5′-TCAGGACTCCACTTACTAGCTTCACG-3′; Schuettpelz & Pryer 2007) and two internal primers: 636F (5′-GCGTTGGAGAGATCGTTTCT-3′; Renner 1999) and F673R (3′-TTCAGCCTGGGATTTGAAAAG-5′; Wolf *et al.* 1994). The *trnL-trnF* IGS was amplified and sequenced using primers e (5′-GGTTCAAGTCCCTCTATCCC-3′) and f (5′-ATTTGAACTGGTGACACGAG-3′; Taberlet *et al.* 1991). The *atpA* gene was amplified and sequenced using ESATPF412F (5′-GARCARGTTCGACAGCAAGT-3′), ESTRNR46F (5′-GTATAGGTTCRARTCCTATTGGACG-3′), ESATPA535F (5′-ACAGCAGTAGCTACAGATAC-3′) and ESATPA557R (5′-ATTGTATCTGTAGCTACTGC-3′) (Schuettpelz *et al.* 2006). Amplification of the *rbcL* gene was carried out in PCR system 9700 machine with a reactions volume of 25 µl containing 22.5 µl 2.5 mM $MgCl_2$ PCR master mix (Abgene Ltd., Epsom, U.K.), 0.5 µl bovine serum albumin (BSA; 0.04%), 50 ng of each primer with a varying amount (ca 1 µl) DNA template, depending on the origin of the sample. PCR procedures were as follows: initial template denaturation at 94°C for 5 min, followed by 30 cycles of denaturation at 94°C for 1 min, primer annealing at 45°C for 1 min, extension at 72°C for 2 min, and ending with a final extension of 10 min at 72°C. The amplification of the *trnL-trnF* IGS was carried out in 25 µl reactions, containing 22.5 µl 2.5 mM $MgCl_2$ PCR master mix, 0.5 µl 0.04% BSA, 50 ng each primer and ca. 1 µl DNA template. PCR procedures were as follows: initial denaturation at 94°C for 2 min, followed by 35 cycles of denaturation at 94°C for 1 min, annealing at 52°C or 56°C for 1 min, extension at 72°C for 3 min and ending with a final extension of 7 min at 72°C. Finally, the amplification of *atpA* was carried out in 25 µl reactions, containing 22.5 µl 2.5 mM $MgCl_2$ PCR master mix, 0.5 µl 0.04% BSA, 50 ng of each primer and ca. 1 µl DNA template. Temperature and cycling condition for PCR amplification were as follows: one 94°C denaturation cycle for 3 min, followed by 30 cycles of 94°C denaturation for 45 sec, annealing at 52°C for 30 sec and elongation at 72 °C for 90 sec and one terminal elongation at 72 °C for 5 min (Pryer *et al.* 2001, Schuettpelz *et al.* 2006).

PCR products were purified using DNA purification columns according to the manufacturers' protocols (QIAquick; Qiagen Ltd., Crawley, U.K.), then directly sequenced. DNA sequencing was conducted using the chain termination method and ABI Prism Big Dye v.3.1 reaction kit, following the manufacturers' protocols (Applied Biosystems Inc., Warrington, U.K), using the same primers that were used for amplification. The resulting sequences were deposited in GenBank. Sequence data of several Polypodiaceae (eupolypod I) subfamilies and three representatives of Hypodematioideae and Didymochlaenoideae (for outgroup comparison) were downloaded from GenBank for use in analyses (see Table 1 for GenBank accession numbers).

Phylogenetic inference

Sequences were edited and subsequently aligned using MUSCLE (Edgar 2004) in Geneious Pro 6.1 and the incomplete 5′ and 3′ ends of each partition were pruned based on visual inspection of the alignments. Data matrices were concatenated using the Bioedit v. 7.09.0 software (Hall 1999). Single-partition (*atpA*, *rbcL*, *trnL-F* IGS) and combined phylogenetic inferences were conducted employing maximum parsimony (MP) analyses and Bayesian Markov chain Monte Carlo (MCMC) analyses. Maximum parsimony analyses were performed with PAUP* 4.0b10 (Swofford 2003) using 1000 random stepwise heuristic searches and TBR branch swapping. All characters were unordered and equally weighted. In the case of the Bayesian analyses, the best-fitting substitution model for each DNA region (*rbcL*, *trnL-F* IGS, *atpA*) was selected using MrModeltest2 (v2.3; Nylander 2004) based on the Akaike information criterion (AIC).

Bayesian inference (BI) analyses were carried out using MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003). Once the best sequence evolution model was determined (Table 2) analysis was conducted using posterior probability (PP) estimated with four chains, each for 100 0000 generations, sampling every 1 000 generations. For each of the individual data partitions and the combined dataset, the first 2 500 samples from each run were discarded as burn-in to ensure that the chains reached stationarity.

Didymochlaena Desv. and *Hypodematium* Kunze were used as outgroups, because in previous analyses (e.g. Lehtonen 2011) they were identified as sister to all other eupolypods I (= Polypodiaceae *sensu* Christenhusz & Chase 2014).

TABLE 2. Statistics for the four datasets analyzed in this study.

Data set	Included taxa	Included characters	Variable characters[1]	Potentially informative characters	Tree length	CI	RI	RC	Best-fitting model[2]
*rbc*L	80	1187	124 (11%)	306	1247	0.4234	0.7277	0.3081	GTR+I+G
trnL-F IGS	69	593	87 (15%)	263	1310	0.4634	0.6612	0.3064	GTR+I+G
*atp*A	66	1782	179 (10%)	468	1513	0.4409	0.7462	0.3822	GTR+I+G
3-region[3]	80	3562	393 (11%)	1037	4137	0.4627	0.7093	0.3281	GTR+I+G

[1] Among included characters.

[2] As identified with the AIC in MrModelTest.

[3] Combined *rbcL*, *trnL-F* IGS and *atpA*.

Results

The aligned *rbcL*, *trnL-F* IGS and *atpA* datasets had 1187, 593 and 1782 characters, respectively. Table 2 summarizes the number of variable and potentially parsimony-informative sites and tree statistics for the various datasets. The combined dataset consisted of 3562 characters, of which only 393 were variable and 1037 were potentially parsimony-informative.

In the three molecular markers used in this study, the *atpA* dataset was longer than that of the *rbcL* and the *trnL-F* IGS, but the percentage of variable characters from *atpA* and *rbcL* was similar (Table 2). When analysed separately, the different genes did not produce incongruent tree topologies and no strongly supported nodes were in conflict among the trees (results not shown). Therefore, the phylogenetic relationships presented below are based on analyses of the combined data set.

The trees obtained from the BI analyses had similar topology as the MP strict consensus tree (Fig. 1), although the resolution and branch support varied. Tree topology of combined *rbcL*, *trnL-F* IGS and *atpA* datasets was well resolved and internal nodes had higher branch support than the separately analysed genes.

Subfamilies Tectarioideae and Dryopteridoideae were resolved as separate lineages with strong Bayesian posterior probability (100%) support, although the bootstrap values were relatively low. Dryopteridoideae were divided into three clades in our analysis. The first is composed of the traditional members of Dryopteridaceae: *Arachniodes* Blume, *Dryopteris* Adans., *Lithostegia* Ching, *Olfersia* Raddi, *Polystichopsis* (J.Sm.) Holttum, *Polystichum* Roth and *Stigmatopteris* C.Chr., but this clade is poorly supported (BS = 100%, PP = 41%). The second clade had strong support and is composed of species previously placed in Tectariaceae (*Ctenitis* and *Pseudotectaria*) with strong support (BS = 100%, PP = 100%). The third clade had intermediate support (BS = 100%, PP = 81%) and consists of *Lomagramma* J.Sm., *Megalastrum*, *Rumohra* and *Pleocnemia*. Lomariopsidoideae were resolved as sister to Tectarioideae. After the exclusion of *Ctenitis*, *Pleocnemia* and *Pseudotectaria*, Tectarioideae were resolved as monophyletic with strong support.

Arthropteris (including *Psammiosorus*) was strongly supported as sister to the remaining Tectarioideae. The second lineage in Tectarioideae is formed by *Pteridrys*, followed by a well-supported lineage (BS = 100%, PP = 96%) comprising *Triplophyllum*, *Hypoderris brownii* and *Tectaria brauniana* (H.Karst.) Christensen (1934:177), with the latter two as sisters. Within *Triplophyllum*, the two African species form a grade leading up to a strongly supported American clade (BS = 100%, PP = 99%).

The remaining taxa form a strongly supported monophyletic clade that mostly consists of *Tectaria*; *Cionidium, Ctenitopsis, Dictyoxiphium, Fadyenia, Hemigramma*, *Podopeltis* and *Quercifilix* are deeply embedded in it. *Tectaria* consists of two main clades. One is composed of Palaeotropical taxa (*Tectaria* I) and the other contains both a Palaeotropical lineage (*Tectaria* III, including *Cionidium*) and a Neotropical lineage (*Tectaria* II).

Discussion

Monophyly of Tectarioideae

Our results are in line with the suggestion that Tectarioideae *sensu* Holttum (1947) are polyphyletic. The placement of *Cyclopeltis* in subfamily Lomariopsidoideae (Smith *et al.* 2006, Schuettpelz & Pryer 2007) is supported by our analyses, as is the inclusion of *Dryopsis* and *Ctenitis* in Dryopteridoideae (Li & Lu 2006, Liu *et al.* 2007). Indeed, *Dryopsis* has already been merged with *Dryopteris* (Zhang 2012), although this may cause *Dryopteris* not to be monophyletic (Christenhusz & Chase 2014). *Ctenitis* (including *Ataxipteris*) forms a lineage with *Pseudotectaria* and both are deeply embedded in Dryopteridoideae, even though these three genera share morphological characteristics with Tectarioideae and were associated with it previously. *Pleocnemia*, which was placed in Tectariaceae by Smith *et al.* (2006) and Christenhusz *et al.* (2011), is here shown to belong to Dryopteridoideae, agreeing with other recent studies (e.g. Liu *et al.* 2014). With the exclusion of these genera, Tectarioideae are monophyletic and are composed of *Arthropteris*, *Pteridrys*, *Triplophyllum*, *Hypoderris* and *Tectaria*. We were not able to sample *Aenigmopteris*, so its placement remains uncertain.

Phylogenetic position of *Pseudotectaria*

Traditionally, *Pseudotectaria* has been associated with Tectarioideae (Tryon & Tryon 1982). It has frequently been considered a synonym of *Tectaria* (Kramer *et al.* 1990, Smith *et al.* 2006), but it has also been thought to have a close relationship with *Ctenitis* or *Dryopsis* (Holttum & Lin 1990, Holttum & Edwards 1986). Indeed, *Pseudotectaria* appears morphologically intermediate between *Tectaria* and *Ctenitis*. Like *Tectaria* the veins of *Pseudotectaria* are (occasionally) anastomosing, the blades lacks glands and rhizomes bear narrowly lanceolate, clathrate or non-clathrate scales. *Pseudotectaria* resembles *Ctenitis* in the usual presence of short ctenitoid hairs, the occasionally free venation, the spore ornamentation (Holttum 1983) and their basic chromosome number (both $x = 41$; Holttum & Lin 1990). In our molecular phylogenetic analysis, the *Pseudotectaria* samples form a clade with *Ctenitis*, strongly supporting the placement of *Pseudotectaria* in Dryopteridoideae. A more complete sampling of the *Ctenitis* lineage will be needed to find the exact placement of *Pseudotectaria* in the ctenitoid lineage.
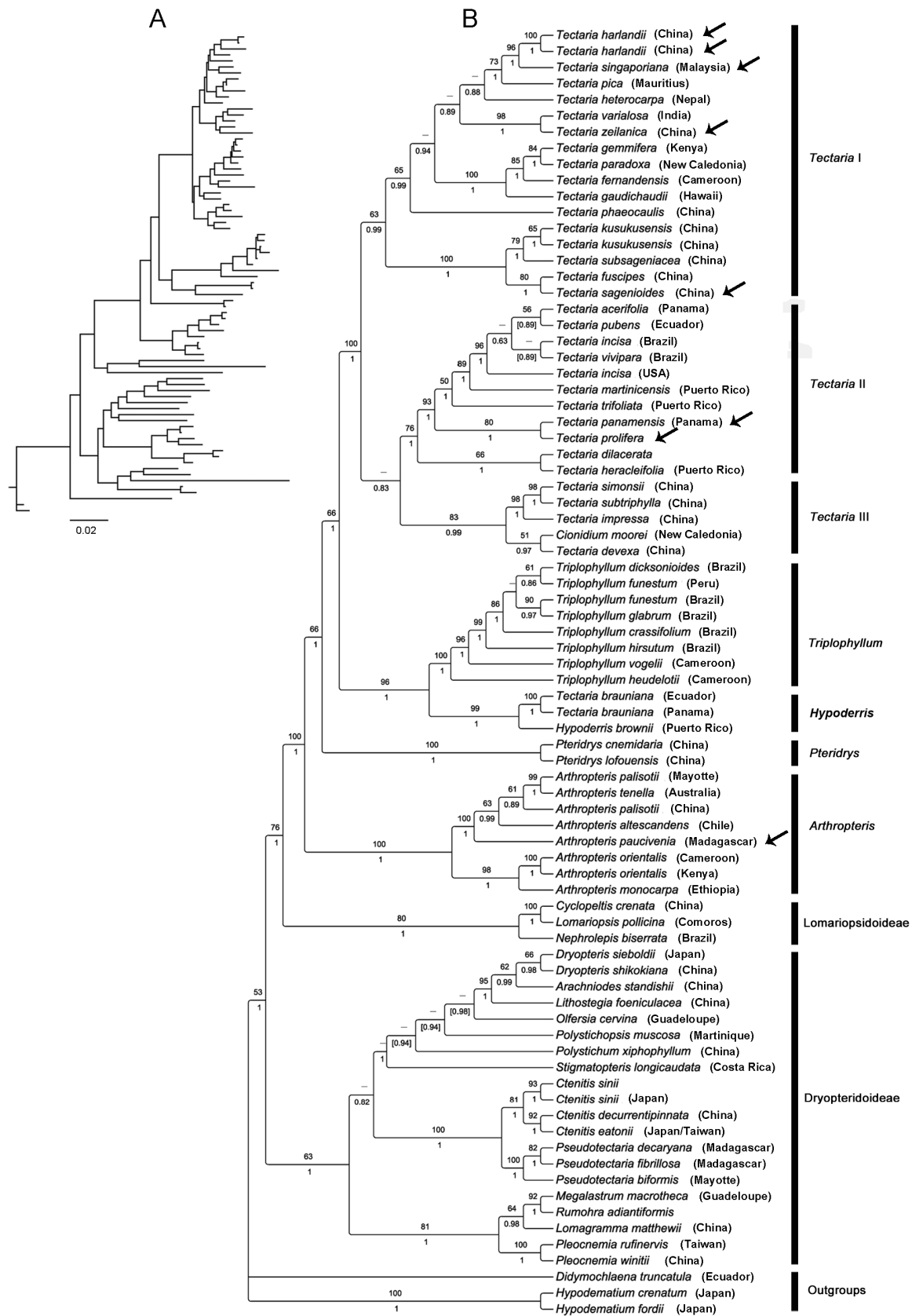
FIGURE 1. Phylogenetic relationships of species associated with *Tectaria* based on plastid DNA markers (*atpA, rbcL* and *trnL-F* IGS). A. Bayesian inference (BI) phylogram showing branch lengths; B. Fifty percent majority-rule consensus tree resulting from parsimonious analyses. Maximum parsimony (MP) bootstrap percentages are shown above the corresponding branches and posterior probabilities (PP) are given below the branches. Square brackets indicate nodes that do not appear in the BI phylogram. Dashes indicate MP bootstrap values of less than 50%. Arrows indicate accessions of genera previously segregated from *Tectaria*, from top to bottom *Hemigramma* (2 samples), *Podopeltis, Quercifilix, Ctenitopsis, Dictyoxiphium* and *Fadyenia*, and *Psammiosorus* formerly segregated from *Arthropteris*.

Phylogenetic position of *Hypoderris*

Previous authors have proposed a relationship between *Hypoderris* and *Woodsia* (e.g. Hooker 1838) or segregated *Hypoderris* as its own family (Ching 1940). The latter emphasizes its unique basal indusium. The lamina of *Hypoderris* is deeply lobed and the sori are relatively small, similar to other Neotropical *Tectaria* spp. (Tryon & Tryon 1982). *Hypoderris* differs from most *Tectaria* spp. in having long-creeping rhizomes, but shares this character with *T. brauniana* and *Triplophyllum*.

    Tectaria brauniana differs from all other *Tectaria* spp. in having deeply pinnatifid fronds, free veins, creeping rhizomes and presence of minute sessile or subsessile spherical glands on the lower leaf surface and indusia (Holttum 1987). Christensen (1934) considered this species to be intermediate between *Tectaria* and *Ctenitis* on morphological grounds. In the Neotropics, *Tectaria* spp. are found on relatively nutrient-rich soils, but *T. brauniana* is an exception found on intermediate to relatively poor soils. In this respect, *T. brauniana* is similar to *Triplophyllum* (Tuomisto & Poulsen 1996), which it also resembles in general lamina dissection. On the other hand, *T. brauniana* shares morphological characters with *Hypoderris brownii*: both have similar scales and similar articulate hairs along the petioles and rachises. Tryon & Lugardon (1991) showed that both also have prominent, irregular echinate spores.

    Tectaria brauniana and *H. brownii* form a strongly supported monophyletic clade in all our analyses, separate and combined. This clade was rendered sister to *Triplophyllum* with strong support in all analyses except in MP of the *trnL-F* IGS, which resolved it as sister to *Tectaria*. Given that *T. brauniana* and *H. brownii* are closely related, and that together they are most likely sister to *Triplophyllum* rather than *Tectaria*, for monophyly of *Tectaria*, *T. brauniana* needs to be transferred to *Hypoderris*. This new combination is provided below.

Monophyly and evolution of *Triplophyllum*

Triplophyllum comprises about 25 species with a disjunct distribution in the Neotropics and Africa-Madagascar (Moran & Smith 2001, Prado & Moran 2008). Because of this bicontinental distribution, it is a good case to study the biogeographical relationships between rainforest floras of the two continents (see discussion and references in Christenhusz & Chase 2013). Previous phylogenetic analyses based on DNA data have included only a single specimen of Neotropical *Triplophyllum*, placing it as sister to *Tectaria* (Schuettpelz & Pryer 2007). Our phylogenetic analyses corroborated this position, and the additional species from both continents supported considering *Triplophyllum* as monophyletic. However, a more complete sampling of especially the Palaeotropical species is needed to further test this assertion.

    Triplophyllum is similar to *Tectaria* in the vascular structure of rhizomes and the morphology of the scales (Holttum 1986), and like those of many *Tectaria* spp., the spores of *Triplophyllum* have wing-like, echinulate folds (Holttum 1987). *Triplophyllum* has the same chromosome number as *Ctenitis* ($x = 41$), which differs from that of *Tectaria* ($x = 40$). This was probably one of the reasons why *Triplophyllum* was associated with *Ctenitis* in the past.

    Prado & Moran (2008) noticed that scales and lamina dissection are variable in *Triplophyllum*. They stated that the nature and position of hairs were more constant within species than the traditionally employed lamina dissection when distinguishing between species. As in *Hypoderris*, most *Triplophyllum* species have dense or sparse articulate hairs, but *Triplophyllum* species also have non-clathrate scales and short ctenitoid hairs that are not present in *Hypoderris*. In addition, *T. brauniana* has free veins and spherical glands similar to those of *Triplophyllum dicksonioides* (Fée) Holttum (1986: 257). With the long-creeping rhizome, these shared characters support the close relationship between *Hypoderris* and *Triplophyllum* as revealed by our molecular data.

    This similarity raises the question if there are sufficient morphological characters to allow separation of *Hypoderris* and *Triplophyllum*, or if the genera should be combined. Since *Hypoderris* has nomenclatural priority, merging the two genera would necessitate transferring all *Triplophyllum* species to *Hypoderris*. Given that we have only sampled a small part of the species currently assigned to *Triplophyllum* and our sampling does not include the type species of *Triplophyllum*, we refrain from making that decision at this stage.

    Prado & Moran (2008) found that the spores of *Triplophyllum* were consistently monolete with a folded perispore surrounded by small spines, which they interpreted as evidence that *Triplophyllum* spp. in the Neotropics and Palaeotropics form a single lineage. This is supported by our phylogenetic results. Because the African species (*T. vogellii* (Hook.) Holttum 1986: 249 and *T. heudelotii* Pichi-Sermolli 1991: 126) form a grade leading to an American clade, it can be suggested that *Triplophyllum* originated in Africa and then spread to and diversified in the Americas, as Holttum (1986) suggested. On the other hand, the entire clade is sister to the Neotropical

Hypoderris, so it is more likely that the history is more complicated, long-distance dispersal not being uncommon between the two continents (see discussion and references in Christenhusz & Chase 2013).

Relationships within *Tectaria*: the undivided leaves unraveled

Our phylogenetic tree shows that the *Tectaria* clade is composed of three clades all with strong support and each with a different geographical distribution: one is Palaeotropical (*Tectaria* I), one is Neotropical (*Tectaria* II) and one is South-East Asian (*Tectaria* III). *Tectaria* clade III includes the peculiar genus *Cionidium*, an endemic to New Caledonia, which was segregated because of its extramarginal (stalked) sori and lanceolate, non-clathrate scales. Even though Bower (1928) placed *Cionidium moorei* in *Deparia* Hook. & Grev., it resembles *Tectaria* in most other characters, except the sori. Copeland (1947) therefore considered it most closely related to *T. seemannii* (E.Fourn.) Copeland (1929: 359), another New Caledonian species. Our phylogenetic analyses places *Cionidium* with reasonable support in a clade comprised of the South-East Asian species *T. impressa* (Fée) Holttum (1988: 483) and *T. simonsii* (Baker) Ching (1931: 32) and the more widespread *T. devexa* (Kunze) Copeland (1907: 415), which extends into Polynesia.

The Neotropical clade *Tectaria* I includes *T. trifoliata* (L.) Cavanilles (1802: 249), which is the type species of the genus. We also included two samples of *T. incisa* and one of its synonyms, *T. martinicensis* (Spreng.) Copeland (1907: 410). This taxon is variable and taxonomically complex and probably includes more than one species. Indeed, the three specimens were not resolved together, indicating that this species is not monophyletic. A more detailed study of the *T. incisa* complex using morphological and molecular characters will be needed to tease this species complex apart and allow its biogeography to be discussed. Taxonomic study of this species complex is important because of its weedy and invasive nature and possibility of hybridisation with other taxa (Wagner *et al.* 1978, Gordon & Thomas 1997).

Fadyenia prolifera Hooker (in Hooker & Bauer 1840: t53-B) is a Caribbean species that was originally separated from *Tectaria* because of its simple proliferous leaves and peculiar lunate indusia (Hooker & Bauer 1840). Later it was placed in *Tectaria* because of its anastomosing veins forming elongate areoles (Tryon & Tryon 1981), a placement which was corroborated by molecular studies (Schuettpelz & Pryer 2007). In our analyses, *T. prolifera* (Hook.) Tryon & Tryon (1981: 136) was found to be sister to *T. panamensis*, the type species of the segregate genus *Dictyoxiphium*. Since *Dracoglossum* has been excluded from *Tectaria*, *T. panamensis* and *T. prolifera* are the only Neotropical species in the genus with simple leaves. However, separating them from other *Tectaria* spp. at a generic level is not justified according to our results, because their lineage is deeply embedded in the Neotropical clade of *Tectaria*. *Tectaria panamensis* is also known to hybridize with *T. incisa*, resulting in sterile plants with intermediate leaf division (Wagner *et al.* 1978). Because most juvenile sporophyte leaves are simple, it has been suggested that entire leaves in adults belonging to lineages with generally divided leaves are a form of paedomorphy or neoteny, simple leaves having evolved through reduction, as is also seen in Marattiaceae (Stidd 1974, Christenhusz *et al.* 2008, Christenhusz 2010a) and Marsileaceae (Pryer & Hearn 2009).

In *Tectaria* clade I, about four lineages can be recognized, although some with weak support only. The genus *Ctenitopsis* (here represented by *Tectaria fuscipes* (Wall. ex Bedd.) Christensen 1931: 290, *T. kusukusensis* (Hayata) Lellinger 1968: 157, *T. sagenioides* (Mett.) Christenhusz 2010b: 58 and *T. subsageniacea* (Christ) Christenhusz 2010b: 59), has been segregated from *Tectaria* on the basis of partially anastomosing veins and absence of included veinlets (Tardieu-Blot & Christensen 1938). However, in our analyses it forms a well supported clade that is deeply embedded in *Tectaria*. A second set of species with simple leaves showing paedomorphy is found in *Tectaria* clade I: *Tectaria singaporiana* (Wall. ex Hook. & Grev.) Copeland (1917: 368), the type species of former segregate genus *Podopeltis*, is sister to *T. harlandii* (Hook.) Kuo (2002: 173), the latter species previously known as *Hemigramma decurrens* (Hook.) Copeland (1928: 404; see Xing *et al.* 2013). Both species have simple leaves (although they are deeply lobed in *T. harlandii*) and sporangia with confluent sori along the veinlets. This is different from typical *Tectaria* spp., which have sporangia in distinct round sori.

Another segregate genus with simple leaves is *Quercifilix*. This genus has dimorphic leaves with the fertile leaves having laminae that are much contracted and with sporangia placed densely along veinlets. However, *Quercifilix* (*T. zeilanica* (Houtt.) Sledge 1972: 422), *Podopeltis* (*T. singaporiana*) and *Hemigramma* (*T. harlandii*) all have the more or less anastomosing veins that form copious areoles typical of many *Tectaria*. Holttum (1988) did not recognize *Hemigramma* as a natural group, but showed that its species are similar to *Tectaria*. The condition of leaf dimorphism has arisen many times in ferns, in *Tectaria* alone at least eight times according to the

results of our phylogenetic analysis. *Tectaria* also contains species with partial leaf dimorphism: the fertile leaves are otherwise similar to sterile ones, but are more contracted and/or have longer petioles. The segregate genera *Fadyenia, Hemigramma, Podolepis* and *Quercifilix* were all based on leaf dimorphism but are now included in *Tectaria* (Kramer *et al.* 1990, Smith 1995, Schuettpelz & Pryer 2007, Christenhusz *et al.* 2011), and it is more likely that they are derived through reduction and paedomorphy as has been suggested for other fern families (e.g. Asama 1960, Stidd 1974, Pryer & Hearn 2009, Christenhusz 2010a).

Conclusions

On the basis of our phylogenetic study we redefine Polypodiaceae subfamily Tectarioideae to consist of the genera *Arthropteris* (including *Psammiosorus*), *Hypoderris* (including *Tectaria brauniana*), *Triplophyllum* and *Tectaria* (including *Amphiblestra, Bathmium, Camptodium, Cardiochlaena, Chlamydogramme, Cionidium, Ctenitopsis, Dictyoxiphium, Dryomenis, Fadyenia, Grammatosorus, Hemigramma, Lenda, Luerssenia, Microbrochis, Phlebiogonium, Podopeltis, Psomiocarpa, Quercifilix* and *Sagenia*). *Pseudotectaria* is more closely related to *Ctenitis* than to *Tectaria*, and *Pleocnemia* is more related to *Lomagramma, Rumohra* and *Megalastrum*. These genera should be excluded from Tectariaceae. The affinities of *Aenigmopteris* are still uncertain due to lack of DNA samples and should be studied when material becomes available.

Triplophyllum is monophyletic and has proven to have one or more long-distance migration events between Africa and South America, but the direction cannot be ascertained. Whether *Triplophyllum* is distinct from *Hypoderris* remains to be verified. Simple leaves have evolved at least twice in *Tectaria*, so this character is not useful for generic circumscription, although it was commonly used for that purpose in the past. Because there are many examples of fern lineages that include both simple and multiply divided leaves, and that most ferns initially have simple leaves that only become more divided when older, we conclude that simple leaves are cases of paedomorphism (a form of neoteny) in ferns.

Taxonomy

Hypoderris brauniana (H.Karst.) F.G.Wang & Christenh., *comb. nov.*

Basionym:—*Aspidium braunianum* Karsten (1859: 63). Type: Colombia. *Karsten s.n.* (holotype: W?, not seen)
Homotypic synonym:—*Tectaria brauniana* (Karsten) Christensen (1934: 177).
Heterotypic synonym:—*Tectaria neotropica* L.D.Gómez in Gómez & Gómez (1982: 475). Type: Panama. Prov. Coclé, Trail from Río San Juan to Río Tife Falls, *Hammel 3348* (holotype: CR, not seen; isotype: MO!). Paratypes: Panama. *Folsom & al. 6174* (CR, MO!).
Distribution:—Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia.

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