



# Phylogeny and character evolution of the fern genus *Tectaria* (Tectariaceae) in the Old World inferred from chloroplast DNA sequences



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## ABSTRACT

In this study we provide a phylogeny for the pantropical fern genus *Tectaria*, with emphasis on the Old World species, based on sequences of five plastid regions (*atpB*, *ndhF* plus *ndhF-trnL*, *rbcl*, *rps16-matK* plus *matK*, and *trnL-F*). Maximum parsimony, maximum likelihood, and Bayesian inference are used to analyze 115 individuals, representing ca. 56 species of *Tectaria* s.l. and 36 species of ten related genera. The results strongly support the monophyly of *Tectaria* in a broad sense, in which *Ctenitopsis*, *Hemigramma*, *Heterogonium*, *Psomiocarpa*, *Quercifilix*, *Stenosemia*, and *Tectaridium* should be submerged. Such broadly circumscribed *Tectaria* is supported by the arising pattern of veinlets and the base chromosome number ( $x = 40$ ). Four primary clades are well resolved within *Tectaria*, one from the Neotropic (*T. trifoliata* clade) and three from the Old World (*T. subtriphyllo* clade, *Ctenitopsis* clade, and *T. crenata* clade). *Tectaria crenata* clade is the largest one including six subclades. Of the genera previously recognized as tectarioid ferns, *Ctenitis*, *Lastreopsis*, and *Pleocnemia*, are confirmed to be members in Dryopteridaceae; while *Pteridrys* and *Triplophyllum* are supported in Tectariaceae. To infer morphological evolution, 13 commonly used characters are optimized on the resulting phylogenetic trees and in result, are all homoplastic in *Tectaria*.

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## 1. Introduction

*Tectaria* Cav. (Tectariaceae) is a pantropical fern genus with most species growing terrestrially in rain forest. As stated by Copeland (1947: 130), “Nothing about *Tectaria* is more remarkable than the number of species and the diverse groups of species”; *Tectaria* is a large group with extremely diverse morphology. The estimated number of species ranges from 150 (Tryon and Tryon, 1982; Kramer, 1990a) to 210 (Holttum, 1991). *Tectaria* was originally established as a genus for ferns with round sori covered by round indusia (Cavanilles, 1799), but has been applied to many very different groups in the history (Underwood, 1902; Ching, 1931; Holttum, 1991). The definition of *Tectaria* began to become clear after the work by Copeland (1907) and Ching (1931); the former made the first revision on *Tectaria* from Philippines while the latter revised this genus from China and nearby Sikkim Himalaya.

Copeland (1907) and Ching (1931) defined *Tectaria* as having lamina comparatively undissected, mostly in deltoid form and in membranaceous or flaccid texture, veins more or less anastomosing, and sori usually indusiate and covered with reniform or pel-tate indusia. Both authors stressed the affinity of *Tectaria* to *Dryopteris* Adans. and suggested the former would be derived from the latter. To date there is no modern taxonomic treatment on the whole genus except for several regional revisions in the recent decades (e.g., Tagawa and Iwatsuki, 1988; Holttum, 1991; Tryon and Stolze, 1991; Wang, 1999; Chandra, 2000; Xing et al., 2013). Holttum (1991) recognized 105 *Tectaria* species from Malesia and considered SE Asia the point of origin of *Tectaria*.

Though widely accepted as a genus since early 1900s, the circumscription of *Tectaria* is very different among authors. Some authors, e.g., Copeland (1960), Pichi Sermolli (1977), Ching (1978), and Wang (1999), adopted *Tectaria* in a narrow sense. They limited *Tectaria* for plants with monomorphic fronds, veins fully anastomosing, and sori being separate, round, and covered with indusia. On the contrary, other authors (Holttum, 1986a; Kramer, 1990a; Smith et al., 2006) took *Tectaria* in a broad sense

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by including some groups with dimorphic fronds and acrostichoid sporangia (*Hemigramma* Copel., *Quercifilix* Copel., *Stenosemia* C. Presl, etc.) and including plants with free veins that used to be grouped into *Ctenitopsis* Ching ex Tardieu & C. Chr. (Tardieu-Blot and Christensen, 1938). Table 1 lists *Tectaria* and allied genera which were variously treated by authors, as well as main characters, richness, and the distribution of each taxon. Of quite a few satellite genera of *Tectaria*, *Ctenitopsis* is the most controversial, which was recognized as a natural group for plants with free or partly free veins and with comparatively finely dissected fronds (Ching, 1938; Tardieu-Blot and Christensen, 1938). However, Holttum (1988, 1991) emphasized the different shape of basal pinna and considered *Ctenitopsis* as a mixture of two other genera. He argued that the species in *Ctenitopsis* with basal pinnae of deltoid shape (basal basicopic pinnules or lobes produced) should be remained in *Tectaria* and the species with basal pinnae of lanceolate shape (basal basicopic pinnules or lobes reduced) should be included in *Heterogonium* C. Presl. (Holttum, 1988, 1991). For the current state of the circumscription of *Tectaria*, Smith et al. (2006: 718) aptly commented that “generic limits, especially within *Tectaria* s.l., are still very much in doubt.”

For the subdivision of *Tectaria*, Ching proposed two sections, four series, and four groups (Ching and Wang, 1983). The section *Tectaria* is featured by having large sori, sori terminal on free veinlets included in areoles, and by having large, persistent indusia; while Sect. *Myriocarpos* Ching has different sori which are smaller, dorsal on anastomosing veins, and are covered by small, caducous

indusia (Ching and Wang, 1983). Ching's series and groups established under the two sections were based on such characters as venation pattern, stipe winged or not, and shape of apical lamina. Different from Ching's opinion, Holttum (1986a) divided *Tectaria* s.l. just into two sections based on the venation, i.e., Sect. *Tectaria* (having fully anastomosing veins, with free veinlets included in areoles) and Sect. *Sagenia* (C. Presl) Holttum (having either free veins, or veins partly anastomosing to form costal areoles, without free veinlets in costal areoles). Due to the lack of analyses on the evolution of morphological characters in *Tectaria*, different authors emphasized the taxonomic values of different characters, which caused wide disagreements on the circumscription and the subdivision of this genus.

Phylogenetic analyses in the recent years, which involved a few samples of tectarioid ferns, threw some unexpected insights on the relationship between *Tectaria* and variously related genera. *Tectaria* has long been thought closely related to *Ctenitis* C. Chr. as they are similar in many characters, especially the fronds covered with ctenitoid hairs and the axes being flat or prominent on both sides. *Ctenitis* was postulated having immediate affinity of, or being a parent group of *Tectaria* (Copeland, 1947; Pichi Sermolli, 1977). These two genera (*Tectaria* and *Ctenitis*) as well as *Lastreopsis* Ching, *Pleocnemia* C. Presl, and *Pteridrys* C. Chr. & Ching were considered as the main components of either Aspidiaceae s.str. (=Tectariaceae) (Ching, 1978; Wang, 1999), Tectarioideae in Dennstaedtiaceae (Holttum, 1947), or Tribe Tectarieae in Dryopteridaceae (Kramer, 1990a). However, the analyses of three cpDNA

**Table 1**

*Tectaria* and allied genera recognized (in boldface) in different classifications, with data on their main characters, richness, and distribution. The genera treated as synonym of *Tectaria* are in italics. (A question mark (?) means the uncertain treatment of the genus followed.)

Pichi Sermolli (1977)	Tryon and Tryon (1982)	Holttum (1986a)	Kramer (1990a) and Smith et al. (2006)	Distinctive character(s) compared to <i>Tectaria</i> s.str.	Chromosomes	Richness and distribution
<b>Amphiblestra</b>	<i>Amphiblestra</i>	<b>Aenigmopteris</b>	<b>Aenigmopteris</b>	Veins free, fronds finely dissected	Unknown	5 spp., Malesia
<b>Camptodium</b>	<i>Camptodium</i>		<i>Amphiblestra</i> <i>Camptodium</i>	Sori marginal, linear, exindusiate Veins free	Unknown <i>n</i> = 40 (Walker, 1966)	1 sp., Venezuela 2 spp., Caribbean islands
<b>Cionidium</b>	<i>Cionidium</i>	<b>Chlamydogramme</b>	? <i>Chlamydogramme</i> <i>Cionidium</i>	Fronds dimorphic, sori linear, marginal Sori terminal beyond lamina margin, indusia cup-like	Unknown Unknown	2 spp., New Guinea 1 sp., New Caledonia
<b>Ctenitopsis</b>		<i>Ctenitopsis</i> , p.p.	<i>Ctenitopsis</i> , p.p.	Veins free or nearly so, fronds comparatively finely dissected	<i>n</i> = 40 (Kato et al., 1992)	ca. 20 spp., Old World tropics
<b>Dictyoxiphium</b>	<i>Dictyoxiphium</i>		<i>Dictyoxiphium</i>	Sori marginal, linear, with continuous extrorse indusia	<i>n</i> = 40 (Wagner et al., 1978)	1 sp., Neotropics
<b>Fadyenia</b>	<i>Fadyenia</i>		<i>Fadyenia</i>	Veins laxly and rather irregularly anastomosing	<i>n</i> = 40 (Walker, 1966)	1 sp., Caribbean islands
<b>Hemigramma</b>		<i>Hemigramma</i>	<i>Hemigramma</i>	Sori acrostichoid	<i>n</i> = 40 (Mitui, 1976)	6 spp., Tropical E Asia to SW Pacific
<b>Heterogonium</b>		<b>Heterogonium</b>	<b>Heterogonium</b>	Veins free or anastomosing only along main veins, lowest pinna broadest above the base Indusia inferior, ciliate at margin	<i>n</i> = 40 (Manton, 1954) <i>n</i> = 40 (Walker, 1985)	ca. 20 spp., Old World tropics 1 sp., Caribbean region
<b>Hypoderris</b>	<b>Hypoderris</b>		<b>Hypoderris</b>		Unknown	1 sp., Caribbean region
<b>Luerssenia</b>			<i>Luerssenia</i>	Fronds dimorphic, indusia elongate-hippocrepiform	Unknown	1 sp., Malesia
<b>Pleuroderris</b>	<i>Pleuroderris</i>		<i>Pleuroderris</i>	Fronds extremely variable	<i>n</i> = 40 (Wagner et al., 1978)	1 sp. Caribbean region
<b>Psomiocarpa</b>		<b>Psomiocarpa</b>	<b>Psomiocarpa</b>	Veins free, fertile pinnae linear with very small pinnules, exindusiate	<i>n</i> = 40 (Holttum, 1991)	1 sp. Philippines
<b>Pseudotectaria</b>	<i>Pseudotectaria</i>		<i>Pseudotectaria</i>	Veins free or distinctly anastomosing as in <i>Cyclosorus</i> , sori exindusiate	<i>n</i> = 41 (Holttum and Lin, 1990)	8 spp. Madagascar and nearby islands
<b>Quercifilix</b>	<i>Quercifilix</i>	<i>Quercifilix</i>	<i>Quercifilix</i>	Fronds dimorphic, diminutive; sori acrostichoid	<i>n</i> = 40 (Manton and Sledge, 1954)	1 sp., Sri Lanka, Indochina to S China
<b>Stenosemia</b>		<i>Stenosemia</i>	<i>Stenosemia</i>	Fronds dimorphic, veins free to anastomosing, sori confluent	<i>n</i> = 40 (Walker, 1973)	2 spp., Madagascar and Malesia
<b>Tectaria</b> s.str.	<b>Tectaria</b>	<b>Tectaria</b>	<b>Tectaria</b>	<b>Tectaria</b> s.str.: Fronds monomorphic, veins fully anastomosing, sori round and separate on lamina	<i>n</i> = 40 (Manton, 1954; Walker, 1966)	c. 150 spp., Pantropical
<b>Tectaridium</b>		<b>Tectaridium</b>	? <i>Tectaridium</i>	Sterile fronds simple, fertile ones deeply lobed, lobes linear	Unknown	1 sp., Philippines

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