



Podostemaceae of Malesia: taxonomy, phylogeny and biogeography

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Key words

biogeography
Cladopus (syn. *Torrenticola*)
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Terniopsis (syn. *Malaccotristicha*)

Abstract Two genera and four species of *Podostemaceae* in Malesia are enumerated and a key to the species is provided. They are morphologically distinct from each other. *Cladopus javanicus* and *C. nymanii* are endemic to Java and Malesia, respectively, and *C. queenslandicus* occurs in eastern Papua New Guinea and north-eastern Australia. *Terniopsis malayana*, formerly called *Malaccotristicha malayana*, is distributed in Peninsular Malaysia to Peninsular Thailand. Asian *Podostemoideae* including *Cladopus* are a product of secondary diversification following a single migration, while *Tristichoideae* with *Terniopsis* show primary diversification in Asia.

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INTRODUCTION

Podostemaceae is a family of unusual aquatic angiosperms that grow submerged in the rapids and waterfalls during the rainy season, and subsequently become exposed and flower during the dry season when the water-level lowers. They are distributed in the tropics and subtropics of the world, usually in regions under seasonal climate (Van Steenis 1981). The family comprises about 50 genera and 270 species (Cook 1996) but may be larger (Cook & Rutishauser 2007). Subfamily *Podostemoideae* is the most diverse in America and the second most diverse in Africa while one species of *Tristichoideae* occurs in both, whereas *Podostemoideae* is the least diverse but *Tristichoideae* is the most diverse in Asia.

The vegetative and reproductive plants of *Podostemaceae*, in particular Asian species are minute, usually consisting of the secondary (adventitious) prostrate roots adhering to the rock surface and shoots or cluster of leaves adventitious on the flank or the upper surface of the root. The roots are ribbon-like (in Malesian and non-Malesian species), subcylindrical or crustose (both in non-Malesian species). This adaptative body plan is a result of saltational evolution leading to the *Podostemaceae* from the common ancestor of *Podostemaceae* and *Clusiaceae*, which have a normal organization (Rutishauser 1995, Soltis et al. 1999, Gustafsson et al. 2002, Kita & Kato 2005). The small carpels in the reduced flowers with single, 2–3-carpous pistil and 1–3 stamens yield dust seeds (c. 200–600 µm long), which may be dispersed by wind or animals (e.g. birds).

Malesia is poor in species diversity of *Podostemaceae*, compared to the adjacent south-eastern Asian regions, partly due to rarity of suitable habitats with seasonal climate. Among the immediately adjacent regions, Thailand is the richest with 9 genera and 34 described species (Kato 2006a), and Laos is the second richest (Kato & Fukuoka 2002; M. Kato and S. Koi unpublished data). Of the other Asiatic regions, the region comprising Southern India and Sri Lanka is as rich as Thailand.

In this paper, I present a taxonomy of Malesian *Podostemaceae*, using taxonomic treatments on Malesian and related extra-

Malesian floras of the family published separately (Van Steenis 1949, 1972, 1989, Dransfield & Whitmore 1970, Cusset & Cusset 1988a, Cusset 1992, Kato & Hambali 2001, Kato & Kita 2003, Kato 2006a). I also give an overview of the underlying phylogenetic relationships of Malesian and related extra-Malesian species and the biogeographic relationships of the whole *Podostemaceae* (Kita & Kato 2001, 2004a, b, Kato et al. 2003, Kato 2006b, Koi et al. 2008).

I classify Malesian *Podostemaceae* into four species referred to two genera (Table 1). *Cladopus nymanii* H. Möller (1899) was described from West Java as the first record of *Podostemaceae* in Malesia. North-eastern Australian *Torrenticola queenslandica* was added as the second species from Papua New Guinea (Van Steenis 1949) and later transferred to *Cladopus* by Cook & Rutishauser (2001). Dransfield & Whitmore (1970) described *Indotristicha malayana* from Peninsular Malaysia (Van Steenis 1972), which has later been transferred to *Malaccotristicha* (Cusset & Cusset 1988a), to *Tristicha* of a different clade (Cook & Rutishauser 2001), and eventually to *Terniopsis* including *Malaccotristicha* (Kato 2006a) (Table 1). Kato & Hambali (2001) added a fourth species, *Cladopus javanicus* from West Java.

KEY TO MALESIAN SPECIES

1. Flowers 3-merous (tepals forming 3-lobed tube covering flower bud, stamens 3, ovary 3-loculate, stigmas 3), capsule obovoid, 9-ribbed, spathella absent; bracts 2, entire, membranous; leaves oblong-lanceolate, univeined, 3-ranked on short shoots (ramuli) (subfam. *Tristichoideae*) *Terniopsis malayana*
1. Flowers 2-merous (tepals 2 on both sides of stamen, free, linear, inconspicuous, stamen 1, ovary 2-loculate, stigmas 2), capsules globose, smooth-surfaced (not ribbed), flower bud enclosed by envelope called spathella; bracts many, digitate or lobed, thick; leaves simple (linear), lobed or digitate, not veined, 2-ranked or irregularly arranged (subfam. *Podostemoideae*) 2
2. Shoots long (to 9 cm); bracts and leaves trifid with elongate middle lobe and small lateral lobes *Cladopus queenslandicus*

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Table 1 Taxonomic treatments of Malaysian *Podostemaceae*.

Van Steenis (1949, 1972, 1989)	Cusset & Cusset (1988a) Cusset (1992)	Kato (2006a, present study)
<i>Cladopus nymanii</i> s.l.	<i>Cladopus nymanii</i> s.l.	<i>Cladopus nymanii</i> s.s. <i>Cladopus javanicus</i> *
<i>Torrenticola queenslandica</i> <i>Indotristicha malayana</i> ***	(not treated) <i>Malaccotristicha malayana</i>	<i>Cladopus queenslandicus</i> ** <i>Terniopsis malayana</i>

* Described by Kato & Hambali (2001)

** Transferred by Cook & Rutishauser (2001)

*** Described by Dransfield & Whitmore (1970)

- 2. Shoots short or long; bracts digitate; leaves simple or digitate. 3
- 3. Vegetative shoots short, comprising clusters of simple leaves; floriferous shoots to 1 cm long, capsules 1–2 mm long. *Cladopus nymanii*
- 3. Vegetative shoots to 5 cm long, as long as reproductive shoots, both bearing numerous digitate leaves, capsules 2–3 mm long *Cladopus javanicus*

Taxonomy

1. *Cladopus nymanii* H.Möller — Fig. 1a, 2

Cladopus nymanii H.Möller (1899) 115, f. 12–15; Steenis (1936) 532, f. 1, 2; (1949) 66, f. 1; (1972) 963, p.p.; Chun & Tsiang (1963) 261, p.p.; T.L.Wu (1964) 373, p.p.; (1988) 6, p.p.; C.Cusset (1992) 22, p.p.; H.X.Qiu & C.T.Philbrick (2003) 191, p.p.
Cladopus warmingiana Koidz. (1929) 52.

Distribution — Java (east to west), Flores, southern Sulawesi, East Kalimantan (?).

Notes — This species has been considered in a broad sense to be variable and widely distributed in eastern and south-eastern Asia (Chun & Tsiang 1963, Wu 1964, 1988, Van Steenis

1972, Cusset 1973, 1992, Qiu & Philbrick 2003). It has included *C. austrosatsumensis* (Koidz.) Ohwi, *C. chinensis* (H.C.Chao) H.C.Chao, *C. doianus* (Koidz.) Kôriba, *C. fallax* C.Cusset, *C. fukienensis* (H.C.Chao) H.C.Chao, *C. japonicus* Imamura and *C. warmingiana* Koidz. However, *C. nymanii* s.s. and *C. fallax*, along with distinct species, are phylogenetically placed in the south-eastern Asian clade (Fig. 3, SE), while *C. doianus*, *C. fukienensis* and *C. japonicus* belong to the eastern Asian clade (Fig. 3, E), indicating that *C. nymanii* s.l. is a heterogenous assembly (Kita & Kato 2001, 2004a, Kato & Kita 2003). The molecular and morphological data show that *C. nymanii* s.s. is restricted to Malesia, although East Kalimantan plants remain to be analyzed.

Cladopus nymanii s.s. has wide ribbon-like roots, relatively long flowering shoots, digitate bracts, and longer stamens than ovaries. By a set of these characters, it differs from the species that have been included in *C. nymanii* s.l. (Table 2). *Cladopus nymanii* is also distinct from other related south-eastern Asian species, e.g., *C. taiensis* C.Cusset with 3–4-lobed bracts and *C. pierrei* (Lecomte) C.Cusset with two stamens (vs one in *C. nymanii*) (Table 2; Cusset 1992, Kato 2006a).

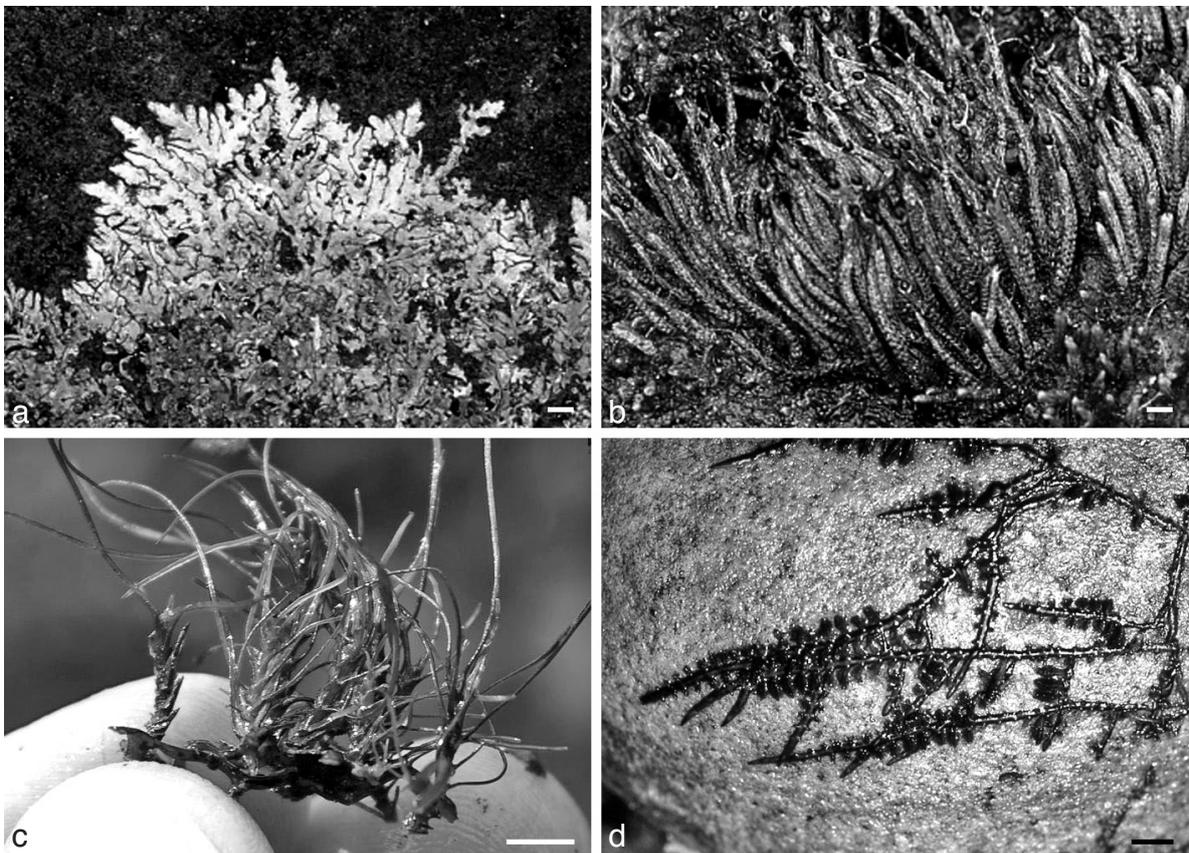


Fig. 1 Malaysian *Podostemaceae* in nature. a. *Cladopus nymanii* in southern Sulawesi: exposed, dried, creeping, branched ribbon-like roots adhering on rock surface; b. *Cladopus javanicus* in western Java with erect shoots on roots (beneath shoots, not seen); c. *Cladopus queenslandicus* in eastern Papua New Guinea: lateral view of creeping root with erect shoots, taken with fingers. Leaves are trifid with elongate middle lobe; d. *Terniopsis malayana* in western Malaysia: branched root with adpressed short shoots on flank. Plant adhering on rock surface was originally submerged. — Scale bars = 5 mm.

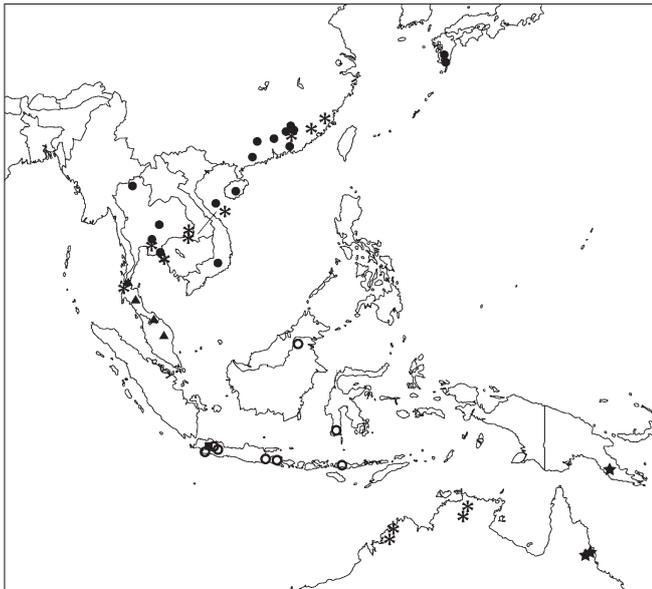


Fig. 2 Map showing distribution ranges of Malesian species: ○ = *Cladopus nymanii*; ● = extra-Malesian species of *Cladopus*; ■ = *Cladopus javanicus*; ★ = *Cladopus queenslandicus*; ▲ = *Terniopsis malayana*; * = extra-Malesian species of *Terniopsis*.

2. *Cladopus javanicus* M.Kato & Hambali — Fig. 1b, 2

Cladopus javanicus M.Kato & Hambali (2001) 98, f. 1–3.

Distribution — West Java.

Note — This species is closely related to *C. nymanii* and occurs within the distribution range of it, but differs considerably in the elongate shoot, as well as the larger flower and fruit (see Key and Table 2). It is also closely related, and similar, to *C. queenslandicus* in the monomorphic vegetative and reproductive shoots. The leaves (bracts) are digitate in *C. javanicus*, whereas they are trifid in *C. queenslandicus*. This monomorphism is distinct from dimorphism in other species of *Cladopus* with digitate or lobed bracts on the reproductive shoot and simple linear leaves on the vegetative shoot (Kato & Hambali 2001, Kato 2006a). Further comparison with collections of young plants is necessary to verify the shoot monomorphism in *C. javanicus* and *C. queenslandicus*.

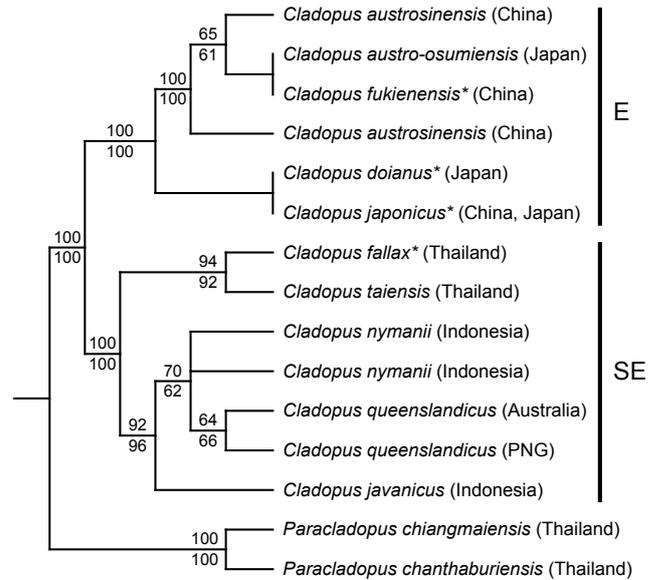


Fig. 3 Phylogenetic relationship of *Cladopus*, based on Kita & Kato (2004a) and Koi et al. (2008). Numbers above and below branches indicate bootstrap values (> 50%) by maximum parsimony and maximum likelihood methods, respectively. Asterisks indicate species that were regarded as conspecific with *C. nymanii*. E = eastern Asian clade; SE = south-eastern Asian clade.

3. *Cladopus queenslandicus* (Domin) C.D.K.Cook & Rutish. — Fig. 1c, 2

Cladopus queenslandicus (Domin) C.D.K.Cook & Rutish. (2001) 1163 — *Torrenticola queenslandica* (Domin) Domin ex Steenis (1949) 68; Aston (1990) 2.

Distribution — Papua New Guinea (Central District); north-eastern Australia (N Queensland).

Note — This species is distributed disjunctively in Papua New Guinea and Australia. Samples from the two localities differ in a small degree in the *matK* sequences, although the two populations are quite similar morphologically (Koi et al. 2008). The species has long been separated as the monotypic genus *Torrenticola* (Aston 1990), until Cook & Rutishauser (2001) transferred it to *Cladopus*, based partly on molecular evidence (Kita & Kato 2001). The species is distinct among congeners in the trifid leaves (bracts), but similar to *C. javanicus* in the monomorphic, long shoot (see above). *Cladopus queenslandicus* is the most eastern and closely related to *C. nymanii* (Fig. 2, 3; Koi et al. 2008).

Table 2 Comparison of characters in Malesian *Cladopus* species and non-Malesian species that have been considered as conspecific with, or related to, *C. nymanii*.

Species	Distribution	Root width (mm)	Flowering-shoot length (mm)	Bract	Stamen length (mm)	Stamen length relative to ovary
<i>C. nymanii</i>	Indonesia	3–5	≤ 10	Digitate	2–3	≥ 1
<i>C. javanicus</i>	Indonesia	2–4	≤ 70	Digitate	1.5–3	± 1
<i>C. queenslandicus</i>	Papua New Guinea, NE Australia	1.5–2.5	≤ 90	3-lobed	2–3	± 1
<i>C. taiensis</i>	Thailand	2–2.5	≤ 1	3–4-lobed	≤ 1.5	± 1
<i>C. fallax</i> ¹	Vietnam, Thailand	2–2.5	≤ 1	Digitate	≤ 1.5	± 1
<i>C. pierrei</i> ²	Laos, Vietnam	1–2.5	3–8	Digitate	1–1.8	≥ 1
<i>C. austrosinensis</i> ³	China (Hainan, Guangdong)	≤ 1	≤ 3	Digitate	≤ 1.5	± 1
<i>C. fukienensis</i> ⁴	China (Fujian)	≤ 1.3	3.5–6	Digitate	1–1.5	± 1
<i>C. japonicus</i> ⁵	Japan, China (Fujian)	2–4	3–4	Digitate	≤ 1.3	± 1
<i>C. doianus</i> ⁶	Japan	1.5–2.5	3–10	Digitate	1	± 1
<i>C. austro-osumiensis</i> ⁷	Japan	≤ 1	≤ 8	Digitate	1–1.5	± 1

^{1,4,5,6} Treated as conspecific with *C. nymanii* by Cusset (1992).

² Stamen comprises two anthers on forked filaments, by which *C. pierrei* was referred to *Cladopus* sect. *Griffithella* (Cusset 1992).

³ Plants referred to *C. nymanii* by Cusset (1992), before *C. austrosinensis* was described (Kato & Kita 2003).

⁶ Possibly conspecific with *C. japonicus*.

⁷ Possibly conspecific with *C. fukienensis*.

4. *Terniopsis malayana* (J.Dransf. & Whitmore) M.Kato — Fig. 1d, 2

Terniopsis malayana (J.Dransf. & Whitmore) M.Kato (2006a) 19. — *Indotristicha malayana* J. Dransf. & Whitmore (1970) 154, f. 1; Van Steenis (1972) 964, f. 12. — *Malaccotrística malayana* (J.Dransf. & Whitmore) C.Cusset & G.Cusset (1988a) 174. — *Trística malayana* (J.Dransf. & Whitmore) C.D.K.Cook & Rutish. (2001) 1166.

Distribution — Peninsular Malaysia (Pahang, Trengganu); Peninsular Thailand.

Notes — This species has been assigned to *Indotristicha*, *Trística* or *Malaccotrística*, as noted in the above synonymy, but molecular phylogenetic analyses showed that this species, along with close relatives, forms a monophyletic group with *Terniopsis sessilis* H.C.Chao, which belongs to a different clade from *Indotristicha* and *Trística* (Kita & Kato 2001, Kato et al. 2003) (see also below). The species is now settled in the genus *Terniopsis* (Kato 2006a).

Terniopsis malayana is the only Malesian species of subfamily *Trísticoideae*. This species has been considered to be endemic to Peninsular Malaysia, but recent research discovered it from Peninsular Thailand (Fig. 2) (Kato 2006a; see also Cusset & Cusset 1988a: 157). Morphologically it is similar to other congeners of Thailand (Kato 2006a) and China (Chao 1948, 1980, Kato & Kita 2003). Nonetheless, it does not differ from the north-western Australian *Te. australis* (C.Cusset & G.Cusset) M.Kato at the *matK* sequence level, suggesting a geologically recent divergence of the two accompanied with an abrupt morphological change (Kato et al. 2003). In *Te. malayana* the stamens are 3 and the ramuli are usually creeping and rarely branched, whereas in *Te. australis* the stamens are 2 and the ramuli are erect and repeatedly ramified (Dransfield & Whitmore 1970, Aston 1990). These differences had made *Te. australis* assigned wrongly to the genus *Trística*, which is morphologically similar but phylogenetically far (Aston 1990; but see Kato et al. 2003).

PHYLOGENY AND BIOGEOGRAPHY

Kita & Kato (2001) analyzed the phylogenetic relationships of *Podostemaceae* worldwide, using a large dataset of species and *matK* sequences. Results showed that the family comprises three major clades, which correspond to subfamilies *Trísticoideae*, *Podostemoideae* and *Weddellinoideae*, the last two of which are sister to each other (Fig. 4). *Cladopus*, a genus of the Asian *Podostemoideae*, comprises two clades, the eastern

Asian clade and south-eastern Asian clade (Fig. 3). All three Malesian species belong to the latter clade, along with *C. fallax* and *C. taiensis* (Kita & Kato 2004a, Koi et al. 2008). Different from the broad species concept (e.g., Van Steenis 1972, Cusset 1992), Malesian *C. nymanii* should exclude *C. fallax* and all eastern Asian species (Kato & Kita 2003, Kita & Kato 2004a, Kato 2006b) (see also Note under the species). It is also noted that the Malesian species are monophyletic. From the phylogeny and distribution (Fig. 2, 3) it is implied that eastward expansion was involved in the diversification of Malesian *Cladopus*.

The genus *Terniopsis* was described for *T. sessilis* of Fujian province, eastern China (Chao 1948, 1980). It has been reduced as a synonym of *Dalzellia* (Cusset & Cusset 1988a) or separated from *Malaccotrística* (Kato & Kita 2003, Kato et al. 2003). *Terniopsis* and *Malaccotrística* are hardly separable morphologically and form a monophyletic clade (Kita & Kato 2001, Kato et al. 2003). Eventually, the genus *Terniopsis* was taxonomically broadened to include south-eastern Asian and north-western Australian species that had been assigned to *Malaccotrística* (Kato 2006a). Phylogenetically, an undescribed species from Thailand diverges in the middle between the genera, tightly linking the two (M. Kato and S. Koi unpubl. result). This addition increasingly ensures inclusion of *Malaccotrística* into *Cussetia*.

The three clades (subfamilies) show particular distribution patterns. In the current classification, the subfamily *Trísticoideae* comprises five genera, i.e., *Cussetia* (with 2 species), *Dalzellia* (6 spp.), *Indotristicha* (2 spp.), *Terniopsis* (6 spp.) and *Trística* (1 sp.) (Kato 2006a, 2006b). *Terniopsis* is basal and the opposite clade consists of *Trística* and a subclade of *Dalzellia* and *Indotristicha* (Kita & Kato 2001, Kato et al. 2003). *Cussetia* (Kato 2006a), *Dalzellia gracilis* C.J.Mathew, Jäger-Zürn & Nileena (Mathew et al. 2001) and *Indotristicha tirunelveliana* B.D.Sharma, Karthik. & B.V.Shetty (Sharma et al. 1974, Uniyal 1999) necessitate phylogenetic inspection to investigate their biogeography. *Terniopsis* ranges from central-eastern China to Thailand, southern Laos, West Malaysia and to north-western Australia (Fig. 2); *Cussetia* occurs in a narrow region over adjacent eastern Thailand, southern Laos and northern Cambodia; *Dalzellia* is widely distributed in southern India, Sri Lanka, Thailand and northern Laos (S. Koi unpubl. data); *Indotristicha* is endemic to southern India; and *Trística* is intercontinental in Africa and America (Kato 2006a, 2006b). Thus, *Trísticoideae* is primarily an Asiatic group with exceptions of *Terniopsis australis* being north-western Australian and *Trística trifaria* (Bory ex Willd.) Spreng. being Afro-American. *Terniopsis australis* is a close relative to *Te. malayana* (Kato et al. 2003). The phylogenetic pattern suggests that *Trística trifaria*, which is primarily African, migrated from western Africa to America and expanded to a wide range from Central America through South America (Kita & Kato 2004b). Therefore, it is likely that *Trísticoideae* diversified in tropical Asia, followed by westward expansion of the ancestor of *Tr. trifaria* and eventually by further trans-Atlantic migration and colonization (Fig. 4; Kita & Kato 2004b).

Podostemoideae is also pantropical, but shows a distribution pattern different from that of *Trísticoideae*. *Podostemoideae* is the most diverse in America (with ± 155 species), the second most diverse in Africa (± 75 spp.) and the least in Asia (± 40 spp.) (Cook 1996). It is likely that the subfamily diversified first in America, then migrated eastwards to Africa and to Asia (Fig. 4; Kita & Kato 2001, Kato 2006b). In this scenario, *Podostemoideae* exhibit secondary diversification in Africa and Asia, subsequent to single events of transcontinental migration. It is consistent with the affinity of the American *Weddellinoideae* with *Podostemoideae*, though it is monotypic and not diversified.

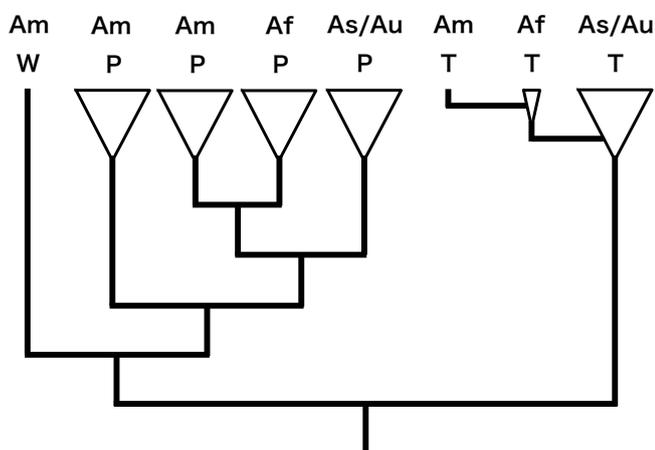


Fig. 4 Simplified phylogenetic relationships of *Podostemaceae*, based on *matK* trees of Kita & Kato (2001, 2004a), Kato et al. (2003) and Koi et al. (2008). The size of triangles does not indicate the degree of species diversity. Af = Africa; Am = America; As = Asia; Au = Australia; P = *Podostemoideae*; T = *Trísticoideae*; W = *Weddellinoideae*.

In conclusion, the family *Podostemaceae* has complicated biogeographical histories. Primary and secondary diversifications occurred in *Tristichoideae* and *Podostemoideae*, respectively, in Asia, whereas secondary diversifications happened in both African subfamilies, and primary diversification happened in *Podostemoideae* and secondary expansion in *Tristichoideae* in America. This scenario is distinct from Cusset & Cusset's (1988b) explanation of the Gondwanic origin of *Tristichoideae*. The deepest divergence of the American *Podostemoideae* and *Weddellinoideae* and the Asian *Tristichoideae* is a challenging subject for the historical biogeography of *Podostemaceae*.

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