

Distribution and Biogeography of Podostemaceae in Asia

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Abstract Podostemaceae are a family of ecologically and morphologically unusual aquatic angiosperms. The distribution maps of Asian Podostemaceae are provided here using results of recent studies, and a biogeographical scenario is proposed based on molecular phylogenetic and distributional data. In the scenario, Podostemaceae or at least Podostemoideae and Weddellinoideae originated in Gondwanaland. Tristichoideae diversified in tropical Asia, with one species migrating westward to Africa and then to South America. Weddellinoideae remained in South America. Podostemoideae diversified first in tropical America and reiterated westward migrations and radiations in Africa with Madagascar and then in Asia. Africa is a passageway for the westward and eastward migrations of the two families.

Key words: aquatic plants, biogeography, distribution, Podostemaceae, Thailand.

Introduction

Podostemaceae are a family of ecologically and morphologically unusual aquatic angiosperms. They occur on rocks in rapids and waterfalls in the tropics and subtropics of the world (Fig. 1) and are distributed in east, south-east and south Asia, Papua New Guinea, north Australia, Africa, Madagascar and adjacent islands, and Central and South Americas (Fig. 2). Central and South Americas harbor about 18 genera and 155 species, while 17 genera and 75 species, and 13 genera and 40 species are distributed in Africa and Asia, respectively (Cook, 1996). The numbers of genera and species are increasing by recent studies and they may reach in total about 300 species. Vegetative plants grow submerged in swift-running water during the rainy season and subsequently emerge and eventually dry during the dry season when the water level drops. Generally flowers open and seeds are set shortly after emergence. Except for a few rootless species, the leading organ of the Podostemaceae plant is the root. It creeps on and adhere to rock surfaces (in some species floating except at the base), is variously flattened ranging from subcylindrical to ribbon-shaped or crustose,

and bears adventitious, both vegetative and reproductive, shoots on the lateral flanks or dorsal side and root hairs (rhizoids) on the ventral surface (Fig. 1) (Willis, 1902b; Troll, 1941; Rutishauser, 1997). Thus, the unusual root is a remarkable adaptation to the unique environment, i.e. the border between hard rock surfaces and fast-running water. Such unique roots were derived from cylindrical, underground roots common in most angiosperms including Clusiaceae (Hypericaceae), which are suggested to be the most closely related eudicot rosoid family (Savolainen *et al.*, 2000; Soltis *et al.*, 1999, 2000; Gustafsson *et al.*, 2002).

The flowers are showy or in more species inconspicuous. The showy flowers with a large number of colored stamens, instead of pale or reduced tepals, are insect-pollinated, while the inconspicuous, small flowers comprising a few reduced tepals, stamens and carpels are primarily wind-pollinated. The seeds are small and avoid of endosperm, due to lack of double fertilization. After imbibition, the seed coats become quickly glutinous to stick on wet rock surfaces, an adaptive character for seed germination in swift-running water. With such seeds Podostemaceae have a long-distance dispersal potential by vectors of



Fig. 1. Podostemaceae in nature. A. *Apinagia* populations in Essequibo River, Guyana. B. *Terniopsis malayana* in Tahan National Park, Malaysia. Roots with short shoots on the flanks creep long on and adhere to rock surface. C. *Polypleurum wallichii* var. *wallichii* in Khao Yai National Park, Thailand. Ribbon-like roots with fascicles of few leaves on the flanks creep on and adhere to rock surface. D. Crustose root of *Hydrobryum japonicum* in Kyushu, Japan. Note linear leaves (red purple) on the dorsal surface of the root. Scale bars=5 mm.

wind, birds, water, or fishes. Nonetheless, most species are restricted to narrow areas, due to hardly identified factors.

I and colleagues have performed floristic studies of Podostemaceae in Thailand and adjacent regions (Kato & Hambali, 2001; Kato & Fukuoka, 2002; Kato & Kita, 2003; Kato *et al.*, 2003; Kato, 2004, in press). They record 34 species in Thailand, six in China, seven in Laos, three in Vietnam, two in Cambodia, and three in Indonesia. There are a few species in north India and Myanmar. Only *Dalzellia* and *Polyleurum* are common genera in Southeast Asia and South Asia. Genera that occur in extra-Thailand are *Indotristicha*, *Hydrobryopsis*, *Willisia*, and *Zeylandium*, all of which are endemic to south India (Mathew & Satheesh, 1997). In comparison, many more genera, i.e. *Cladopus*, *Cussetia*, *Diplobryum*, *Hanseniella*, *Hydrobryum*, *Paracladopus*, *Terniopsis*, and *Thawatchaia*, do not occur in south India and Sri Lanka (Kato, 2004, in press). This paper provides the distribution ranges of Podostemaceae in Southeast Asia with neighboring regions, and a biogeographic scenario of the family.

Biogeography of Podostemaceae

A molecular phylogeny indicates that the family Podostemaceae comprises three subfamilies, Podostemoideae, Weddellinoideae, and Tristichoideae, and the former two form a clade sister to the last (Kita & Kato, 2001). This study and subsequent results (Kato & Kita, 2003; Kato, 2004; Kita & Kato, 2004a, b) also show that clades of the subfamilies are characterized geographically (Fig. 2). Weddellinoideae are monotypic with the sole species *Weddellina squamulosa* occurring in South America. Tristichoideae with ca. 10 species are divided to two clades, *Terniopsis* and a clade of *Tristicha* and a subclade of *Dalzellia* and *Indotristicha*. All genera but *Tristicha* are Asiatic, while *Tristicha* is widely distributed in Africa, Madagascar and South and Central Americas. Podostemoideae, the largest subfamily with ca. 260 species, are divid-

ed to two clades, an American clade and a clade of species occurring in all Asia, Africa and America. The latter clade further diverges into an Afro-American clade and an Asian clade. Hence, the American Podostemoideae are basal and paraphyletic, while the African and Asian are monophyletic.

The phylogeny, along with the distribution patterns and species richness, may suggest a scenario for the historical biogeography of Podostemaceae (Fig. 2): the family originated from a common ancestor with Hypericaceae in an unknown region in Late Cretaceous (72.4–76.4 million years ago; Davis *et al.*, 2005). In this period, Africa and South America, and India and Madagascar had begun to separate by the then less widened Atlantic Ocean, and the northeastwardly drifting India was still far from the Asian continent, isolated by the Tethyan Seaway (Lomolino *et al.*, 2005). The low dispersability of narrowly restricted species (but *Tristicha trifaria*) and the distribution pattern of the family may suggest that the possible place of origin is Gondwanaland or at least part of it. The early Podostemaceae diverged into the Asian Tristichoideae and the American clade consisting of Podostemoideae and Weddellinoideae. After diversification of Tristichoideae in tropical Asia and northward expansion to China, a westward emigrant, i.e. *Tristicha trifaria*, reached Africa and Madagascar with nearby islands (the Reunions and Seychelles) and later South America. Thus, Tristichoideae diversified in Asia and expanded into north Australia, while a single species migrating westward and ultimately to South and Central Americas. The South American Weddellinoideae did not diversify, compared to Tristichoideae and Podostemoideae.

Podostemoideae show a primary diversification in South/Central America, and part of the subfamily migrated to Africa and then to Asia (Fig. 2). The migration took place in the opposite direction to that of Tristichoideae, in the period when the African continental island was separated from South America and also from Asia by the Tethyan Seaway, and India approached and

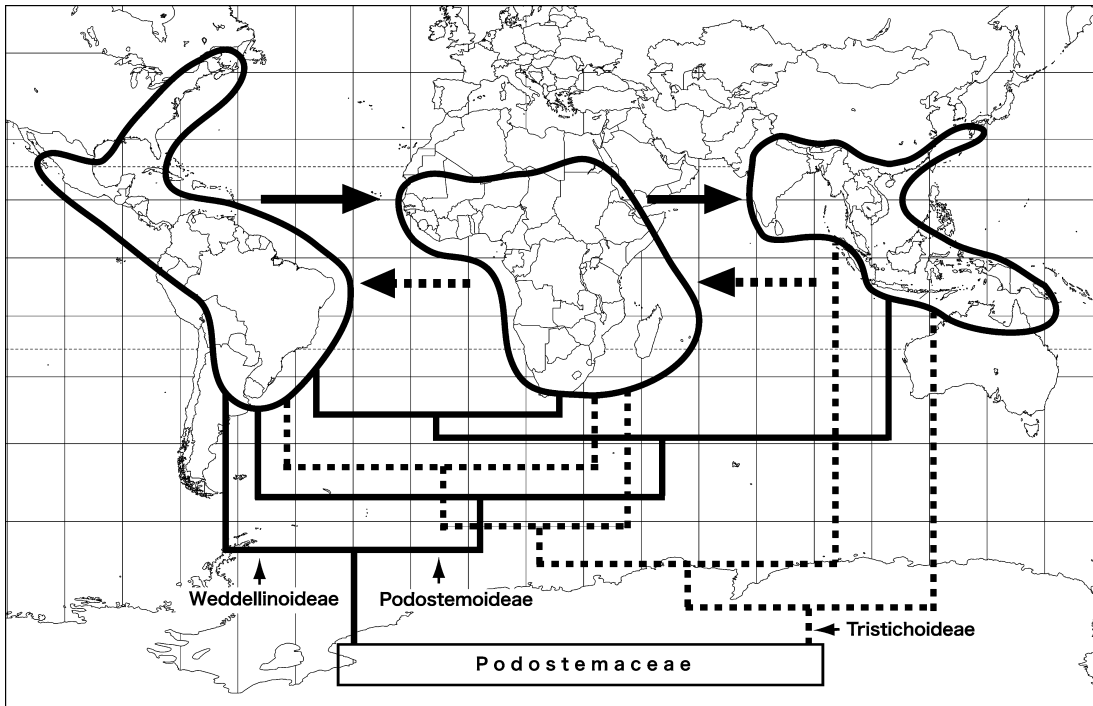


Fig. 2. Distribution map of Podostemaceae with phylogenetic tree adapted from Kita & Kato (2001, 2004a, b), Kato *et al.* (2003), and Kato (2004). Solid and broken lines of tree indicate relationships of Podostemoideae and Weddellinoideae, and Tristichoideae, respectively. Solid and broken arrows indicate intercontinental migrations of Podostemoideae and Tristichoideae, respectively, followed by diversification in each continent.

ultimately collided with the Asian continent (Lomolino *et al.*, 2005). The origin and migration was followed by radiations of the subfamily in each continent. It is noted that American Podostemaceae are a mixture of the originally neotropical Podostemoideae and the immigrating Tristichoideae (*Tristicha trifaria*), along with the endemic Weddellinoideae, while Asian Podostemaceae are a mixture of the primarily Asian Tristichoideae and the secondarily diversified Podostemoideae. Africa is not the place of origin, but a passageway for both the eastward migration of Podostemoideae and the westward migration of Tristichoideae.

The above is a parsimonious scenario for the historical biogeography of Podostemaceae. However, another but non-alternative possibility is not excluded that the present distribution ranges are places of secondary diversification or include them. For example, Asian Tristichoideae may be

of Gondwana origin: the secondary diversification took place in Southeast Asia, subsequent to the primary diversification in India, a part of Gondwanaland, which had begun to split when the Podostemaceae began to evolve. If this is correct, Podostemaceae might have originated in part of Gondwanaland and expanded in different ways via South America (for Podostemoideae-Weddellinoideae) and India (for Tristichoideae).

Both scenarios differ from Cusset & Cusset's (1988) and Les *et al.*'s (1998) hypotheses, although they are similar in the Gondwana origin. Cusset & Cusset (1988) and Les *et al.* (1998) considered that Tristichoideae are a basal clade of Podostemaceae that represents a Gondwana floristic element with *Tristicha trifaria* distributed in Australia, tropical America, Africa, and Madagascar. However, this species is a crown taxon in Tristichoideae and is likely to have very recently migrated from Africa to America (Kita

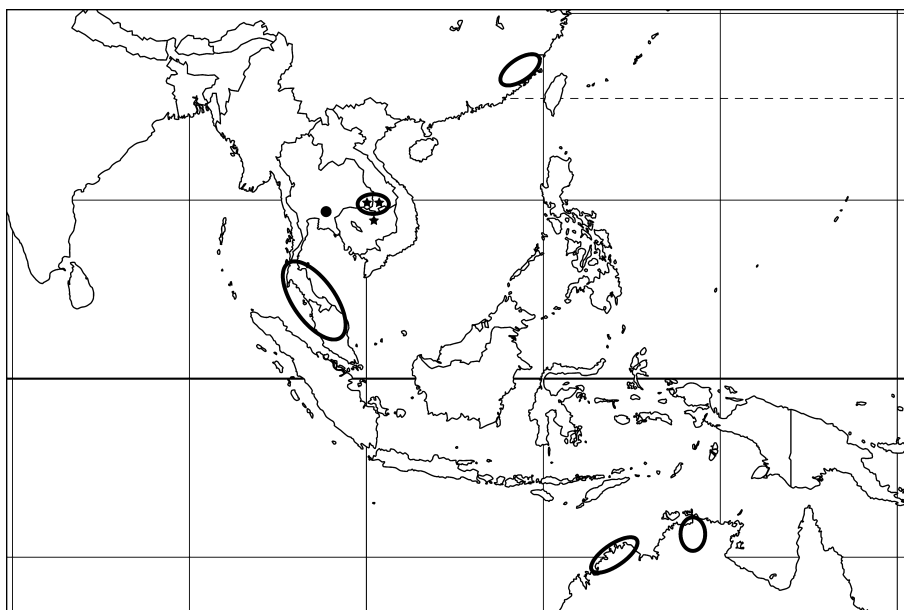


Fig. 3. Distribution map of *Terniopsis* and *Cussetia* (Tristichoideae). Circles and dot indicate *Terniopsis*, and stars, *Cussetia*. *Terniopsis sessilis* occurs in China; *T. malayana*, *T. ubonensis*, *T. brevis*, and *T. ramosa*, in Thailand; *T. malayana*, in peninsular Malaysia; and *T. australis*, in Australia. *Cussetia diversifolia* occurs in Thailand and Laos; and *C. carinata*, in Laos and Cambodia.

& Kato, 2004a), and Australian populations are referred to *Terniopsis australis* (Kato *et al.*, 2003; Kato, in press). Cusset & Cusset (1988) furthermore suggested a northeastward and eastward migration of Tristichoideae, which is in correspondence with our second scenario, although the phylogenetic relationship that underlies their hypothesis may not be correct. Les *et al.* (1998) hypothesized that tropical radiations happened first in South/Central America and second in Asia, based on an *rbcl*-deduced phylogeny. Although they did not examine African species, the hypothesized historical biogeography of Podostemoideae agrees with ours based on a *matK*-deduced phylogeny. From a correspondence of trees deduced from the different genes, it is summarized that reiterated radiations following migrations forced diversification of Podostemaceae in the Cenozoic (Fig. 2).

Distribution Ranges of Genera in Thailand and Adjacent Regions

The taxonomy of species of subfamily Tristichoideae has recently been revised by Kato (in press). Among the five genera assigned to the subfamily, *Cussetia* is endemic to Southeast Asia (eastern Thailand, Laos and Vietnam) (Fig. 3). *Terniopsis* consists of six species, of which four species occur in peninsular, central and eastern Thailand (one species extends south to peninsular Malaysia), *T. sessilis* in central-eastern China, and *T. australis* in the northern part of Northern Territory and Western Australia, Australia (Kato *et al.*, 2003) (Fig. 3). These two extra-Southeast Asian species of *Terniopsis* are not basal in a phylogenetic tree (Kita & Kato, 2001; Kato *et al.*, 2003, Y. Kita, unpubl. results). *Dalzellia zeylanica* and *D. gracilis* occur in south Asia, i.e. southeast India and Sri Lanka (Willis, 1902a, b; Mathew & Satheesh, 1997; Mathew *et al.*, 2001), while four species occur in Thailand (Fig. 4). The remaining genus *Indotristicha* with *I. ramosissi-*

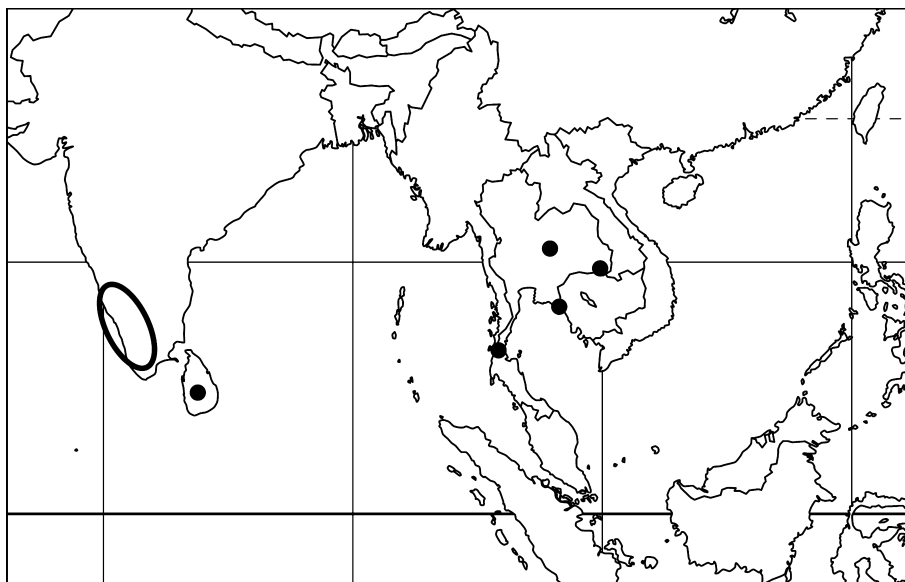


Fig. 4. Distribution map of *Dalzellia* (Tristichoideae). *Dalzellia ubonensis*, *D. ranongensis*, *D. kailarsenii*, and *D. angustissima* occur in Thailand; and *D. zeylanica* and *D. gracilis*, in India and Sri Lanka, and India, respectively. The distribution range of *D. zeylanica* in India almost overlaps with that of *Indotristicha*.

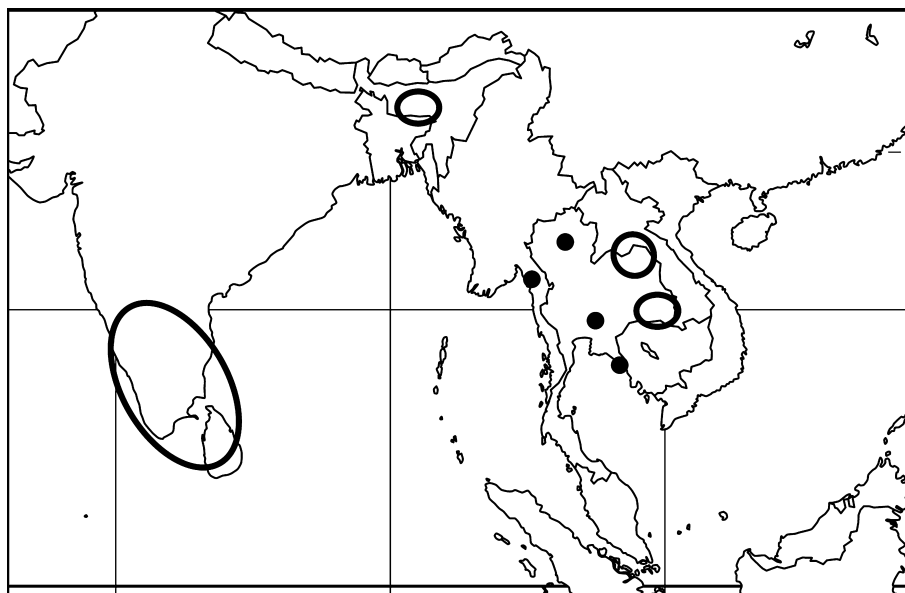


Fig. 5. Distribution map of *Polypleurum* (Podostemoideae). *Polypleurum wallichii* var. *wallichii* and var. *parvum*, *P. schmidianum*, *P. longistylosum*, *P. longifolium*, *P. wongprasertii*, *P. phuwuaense*, *P. rubroradicans*, *P. erectum*, and *P. longicaule* occur in Thailand; *P. wallichii* var. *wallichii* occurs also in India and Laos; *P. filifolium*, *P. munnarensense*, *P. dichotomum*, *P. elongatum*, *P. stylosum*, *P. prostratum*, and *P. disciforme*, in south Asia (India and/or Sri Lanka).

ma and *I. tirunelveliana* occurs in southeastern India. Deduced phylogenetic relationships indicate that the first divergence occurred between *Terniopsis* and the rest of the subfamily. The latter clade diverged into *Tristicha* and a clade of *Dalzellia* and *Indotristicha* (Kita & Kato, 2001, 2004a). *Tristicha* is exceptional in its supercontinental distribution in Africa and America, while all other genera are distributed in Asia and Australia. As aforementioned, the subfamily Tristichoideae diversified first in tropical Asia and later the monotypic Afro-American *Tristicha* migrated to tropical Africa and further to tropical America recently by long-distance dispersal (Kita & Kato, 2001, 2004a).

Concerning the subfamily Podostemoideae, more species (9) of *Polypleurum* occur in Thailand than in South Asia (ca. 7 spp.; Mathew *et al.*, 2003) (Fig. 5). Most of the nine species are endemic to Thailand, but *Polypleurum wallichii*

is distributed in north India, east Myanmar and Laos in addition to Thailand (Kato, in press). As the north Indian-Southeast Asian *P. wallichii* is closely related to the south Asian *P. stylosum* (Kita & Kato, 2001), the phylogeny of *Polypleurum* does not exhibit an obvious geographic pattern. Two species of *Cladopus* occur in Thailand, while several other species are distributed in the surrounding southeastern and eastern Asia (the Indian *C. hookerianus* may not be congeneric) (Fig. 6). The genus comprises an eastern Asian clade distributed in China and Japan, and a Southeast Asian clade distributed in Thailand, Laos, Vietnam, Indonesia, Papua New Guinea, and northeastern Australia. *Paracladopus* with the sole species *P. chiangmaiensis*, endemic to Thailand, is basal in the *Cladopus* clade (Kato, in press). *Cladopus* may be likely to have originated in Thailand or Southeast Asia and expanded to Japan and Australia. In the monophyletic group

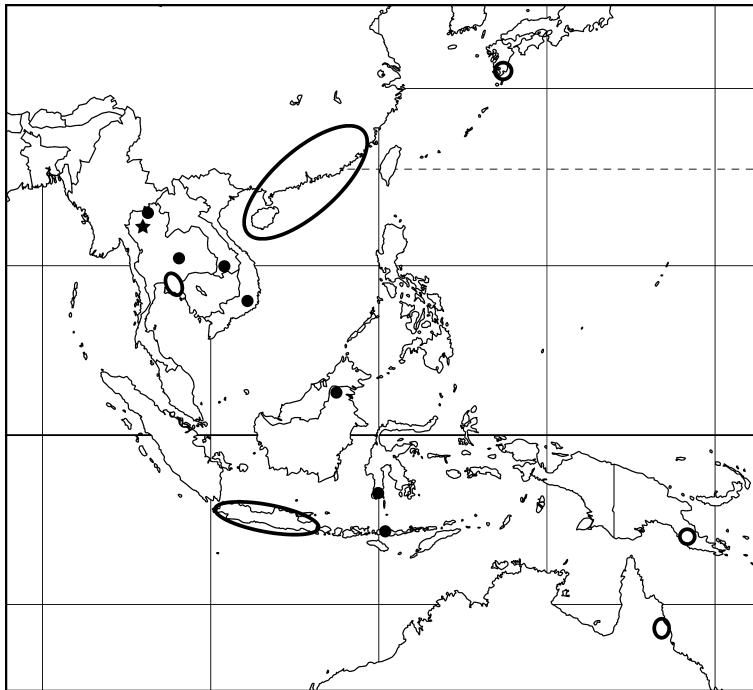


Fig. 6. Distribution map of *Paracladopus* and *Cladopus* (Podostemoideae). *Paracladopus chiangmaiensis* (star), *Cladopus taiensis*, and *C. fallax* occur in Thailand; *C. fallax* and "*C. nymanii*" in Vietnam; *C. pierrei* in Laos; *C. nymanii*, and *C. javanicus*, in Indonesia; *C. queenslandicus*, in Papua New Guinea and Australia; *C. japonicus*, *C. fukienensis*, and *C. austrosinensis*, in China; and *C. japonicus*, *C. doianus*, *C. austro-osumienensis*, in Japan.

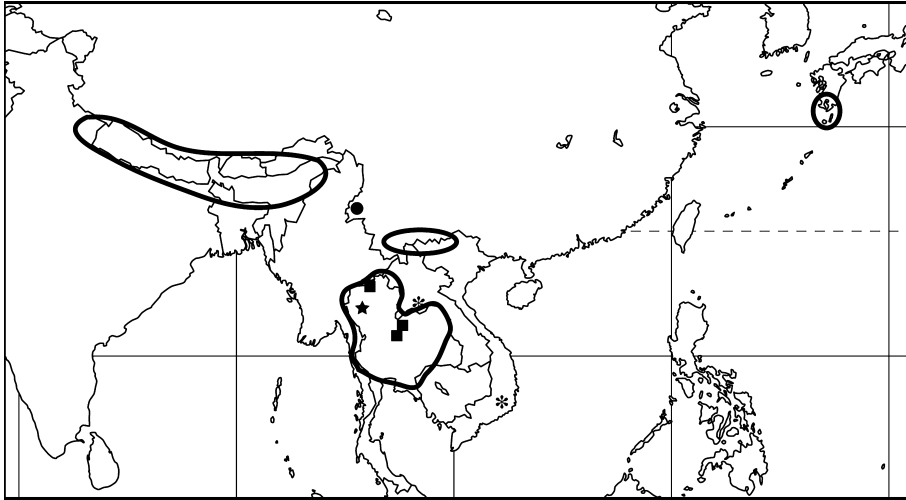


Fig. 7. Distribution map of *Hydrobryum* (circles, dot), *Hanseniella* (squares) and *Thawatchaia* (star) (Podostemoideae). *Hanseniella heterophylla*, *Ha. smitinandii*, *Thawatchaia trilobata*, *Hydrobryum bifoliatum*, *H. kaengsophense*, *H. tardhuangense*, *H. griffithii*, *H. loeicum*, *H. somranii*, *H. chiangmaiense*, *H. japonicum*, *H. khaoyaiense*, *H. micrantherum* var. *micrantherum* and var. *crassum* occur in Thailand; *H. griffithii*, in India and Vietnam; *H. griffithii* and *H. japonicum*, in China; *H. japonicum*, *H. floribundum*, *H. koribanum*, and *H. puncticulatum*, in Japan. *Diplobryum minutale* of southern Vietnam and *D. vientianense* of northern Laos (asterisks), like the three genera, have crustose roots, but their phylogenetic relationships are uncertain.

comprising three crustaceous-rooted genera, most (8) of ca. 11 species of *Hydrobryum* occur in Thailand, and *Hanseniella* and *Thawatchaia* are endemic to Thailand (Kato, 2004) (Fig. 7). The phylogeny that the last two genera are basal in the clade of the crustaceous-rooted genera, and Thai species of *Hydrobryum* are also basal in the genus (Kita & Kato, 2004b), suggests that these crustaceous-rooted genera may have originated in Thailand or Southeast Asia. The present distribution of *Hydrobryum* extending to Japan and the Himalaya may be a result of past northward expansions. Surprisingly, *Hydrobryum japonicum* is distributed disjunctively in Japan, southern Yunnan (China), and northern Thailand, likely due to the subsequent southward dispersal (Kita & Kato, 2004b).

In conclusion, the present distribution of Podostemaceae may be results of both eastward and westward intercontinental migrations of two sub-families in different geological times during the Cenozoic. Thailand with the close adjacent regions, like South Asia, is a core region for the

diversification of all genera of Podostemaceae in Asia, while other regions, e.g. Myanmar, China, Japan, Malaysia, Indonesia, Papua New Guinea, and Australia, are peripheral for their expansions.

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