THAI FOREST BULL., BOT. 50(2): 135–145. 2022.
DOI https://doi.org/10.20531/tfb.2022.50.2.13

Endemism and evolution of Podostemaceae in Phou Khao Khouay National Park, Lao PDR

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ABSTRACT

Podostemaceae of the Phou Khao Khouay National Park and adjoining areas (PKK Area) in Lao PDR were recorded in separate papers, and scattered data make it difficult to gain the whole picture of their diversity and evolution. Our literature research enumerated 18 species and six genera, which account for 43% of species and 55% of genera indigenous to Laos, including 13 PKK Area-endemic species (72%) and three PKK Area-endemic genera (50%). The richness and endemism of species and genera of the PKK Area have the highest density in Asia. Most likely, the genera and all nine endemic species of *Hydrobryum* evolved in the PKK Area. Four endemic species of *Hydrobryum* are ribbon-like/subcylindrical-rooted and sympatric with foliose-rooted congeners. The evolutionary way is opposite to the early one in the ancestor of the *Hydrobryum* clade; the 2-way evolution, together with sympatry, is suggested to be non-adaptive. Two species are perhaps polyphyletic in the initial stage of phylogenetic-species transition. The characteristics of the Podostemaceae found in the PKK Area are important in the context of both biological science and conservation.

KEYWORDS: endemic, hotspot, Phou Khao Khouay NP, Podostemaceae.

Accepted for publication: 8 September 2022. Published online: 25 October 2022

INTRODUCTION

Podostemaceae are a family of flowering plants with an aquatic and lithophytic habit, which generally inhabit rocky waterfalls and rapids in the tropics. The plants grow submerged and adhered to streambed rocks during the rainy season, and as the water level falls in the dry season, the plants become exposed to the air and flower. The rocky habitats are usually patchily distributed even in the same river and sparse among rivers. The algal-like or moss-like extraordinary morphology was used to separate the family as the order Podostemales (Cronquist, 1981; Takhtajan, 2009) or even as the class Podostemopsida (Cusset & Cusset, 1988). However, molecular phylogenetic work indicates that it is sister to the eudicot Hypericaceae (Ruhfel *et al.*, 2011). Moreover, in contrast to relatively small environmental differences among the habitats worldwide, morphological variation is so great that Podostemaceae are classified into more than 300 species assigned to 57 genera (Cook & Rutishauser, 2007; Koi *et al.*, 2019). Therefore, Podostemaceae have great contradictions in ecology, morphology and phylogeny.

Lao PDR, with 42 species and 11 genera, is the second most species-rich country for Podostemaceae in Southeast Asia, following Thailand (Kato, 2018; Koi & Kato, submitted). Podostemaceae occur across Lao PDR, although fewer occur in the northern region than in the southern regions. Current statistics of the genus and species diversity are based on a series of recent taxonomic publications of Lao Podostemaceae (Kato & Fukuoka, 2002; Koi & Kato, 2012, 2015a, b, 2018, 2019, submitted; Koi *et al.*, 2019). The numbers, much larger than four species and three genera recorded in Cusset (1973a, b, 1992) (see also Newman *et al.*, 2007), were increased by new species and records described from across Lao PDR, particularly from the Phou Khao Khouay National Park (area 2,000 km^2, highest peak 1,671 m) and adjoining area (which are located in the same mountain mass and called the PKK Area [Fig. 1]). The PKK Area is located northeast of Vientiane City (https://

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en.wikipedia.org/wiki/Phou_Khao_Khouay) and characterized by a mountainous geography, mostly sandstone-rock geology and tropical monsoon climate. Rivers and streams run in the valleys with many waterfalls and rapids, part of which, such as Tad Leuk and Tad Xai waterfalls, are popular for eco-tourism. Podostemaceae are threatened in various degrees in Lao PDR, and globally, by habitat destruction, such as damming, disruption of currents and water rise and fall, and water pollution (Philbrick *et al.*, 2010; Koi & Kato, 2012; Lansdown, 2012; Cheek & Lebbie, 2018). Lao PDR is included in Indo-Burma, one of the 35 (36 in 2017) biodiversity hotspots recognised for global conservation (Myers *et al.*, 2000; Zachos & Habel, 2011).

The aim of this study was to characterize the Podostemaceae of the PKK Area by integrating the data from separate publications, which made it difficult to recognise the whole picture of the diversity and evolution of the family. It highlights the endemism, phylogeny, speciation and evolution of the family that took place in the PKK Area to evaluate the biodiversity and conservation of the PKK National Park.

MATERIALS AND METHODS

We used the updated data of taxonomy, phylogeny and distribution of Lao Podostemaceae from our field work and previous publications (Kato & Fukuoka, 2002; Koi & Kato, 2012, 2015a, b, 2018, 2019, 2020; Koi *et al.*, 2019), which are gathered together in Koi & Kato (submitted).

RESULTS

Six genera and 18 species of Podostemaceae are recorded from the PKK Area (Table 1, Fig. 2). They inhabit rocky waterfalls and rapids in tributaries of the Mekong River and are scattered across the PKK Area, but are especially dense in the Tad Xai, Tad Leuk and Tad Yong waterfalls in the central part (Fig. 1). Three genera are monotypic and endemic to the PKK Area; that is, *Ctenobryum* Koi, Won & M.Kato (Fig. 2A), *Hydrodiscus* Koi & M.Kato (Fig. 2N) and *Laosia* Koi, Won & M.Kato (Fig. 2P). The other genera are two- or multispecific: *Dalzellia* Wight has two species, of which *D. pseudoangustissima* Koi & M.Kato is endemic to the PKK Area (Fig. 2B), while *D. kailarsenii* M.Kato occurs also in North-Eastern Thailand; *Polypleurum* (Tul.) Warm. has two non-endemic species, *P. pluricostatum* Koi & M.Kato and *P. schmidtianum* Warm. (Fig. 2Q, R; Kato, 2018). Among the 11 species of *Hydrobryum* Endl., nine species are endemic to the PKK Area, while *H. vientianense* (M.Kato & Fukuoka) Koi & M.Kato extends to northern Central Laos and North-Eastern Thailand, and *H. verrucosum* Koi & M.Kato occurs in another location in Khammouane Province, Central Laos (marked with K in Fig. 1) (Fig. 2C–H, J–M). In sum, 13 species (72%) are endemic to the PKK Area.

The species of the Lao *Hydrobryum* clade in the sense of Koi & Kato (2019) are recognised by the morphological characters such as root form and stamen number, and the species of the PKK Area are phylogenetically divided into five sister groups (Table 2; Koi & Kato, 2019). The sister species of sisters 1, 2, 4 and 5 are allopatric, while those of sister 3 are partly sympatric (Fig. 1, Table 2).

DISCUSSION

The Podostemaceae of the PKK Area account for 55% of genera and 43% of species of Laos (Koi & Kato, submitted), although the PKK Area accounts in area for less than 1% of Laos. To our knowledge, the PKK Area shows the highest density of species in Asia among comparatively species-rich areas, such as Khao Yai National Park with seven species in 2,168 km^2 in Central to Eastern and South-Eastern Thailand (Kato, 2006), an east Loei-west Phitsanulok area with 18 species in ca. 10,000 km^2 in North-Eastern to Northern Thailand (Werukamkul *et al.*, 2012, 2018), and Attapeu Province with 12 species in 10,320 km^2 in southern Laos (Koi & Kato, 2012, 2015a, b). In south India, 13 species, or currently a few more, are recorded from Kerala state (38,800 km^2) (Mathew & Satheesh, 1997). Furthermore, most species of the PKK Area (13 of 18 spp., 72%) are endemics of the Area. This narrow endemism is much more prominent than that of the other Lao areas, e.g., five endemic species in Southern Laos, two in Central Laos except the PKK Area, and one in Northern Laos (Koi & Kato, 2012, 2015, 2018, 2019). Nonetheless, the PKK Area does not seem specific in climate, geomorphology and geology to meet the characteristic Podostemaceae.

The three monotypic genera *Ctenobryum*, *Hydrodiscus* and *Laosia* are narrow-endemics, indicating that the PKK Area has the highest density of generic endemism in Asia, probably also in the world. Two monotypic genera exist in nearby waterfalls of Cameroon (Cusset, 1987), two in two individual areas of south India (Koi *et al.*, 2022), one in Sierra Leone (Cheek & Lebbie, 2018), one in Angola (Ameka *et al.*, 2010), one (single collection) in Madagascar (Cusset, 1973c), and one in Brazil (Philbrick *et al.*, 2010), which all are restricted to single rivers or narrow areas, while a dozen other monotypic genera are widely distributed in their own areas (Rutishauser *et al.*, 2007; Ameka *et al.*, 2010; Philbrick *et al.*, 2010; Kato, 2016; Koi *et al.*, 2019). Phylogenetically, *Ctenobryum* and *Hydrodiscus* form a clade, which is allied to the *Hydrobryum* clade (Koi & Kato, 2020). In spite of the sister relationship, *Ctenobryum* and *Hydrodiscus* differ reciprocally in the foliose roots vs. absence of root, multiple vs. single shoot, and digitate vs. entire bracts. Such large gaps probably were generated within the PKK Area by saltation, which is poorly understood, or survival from ancestral multispecific lineages. Geographical isolation might not be effective, because the closest population of *Hydrodiscus* in Tad Xai waterfall (Fig. 1, location code 8) is 8 km apart from the site of *Ctenobryum* (code 9). *Laosia* is unique and characterized by the root-borne thin-columnar organs, which are enigmatic (Koi *et al.*, 2019). Phylogenetically *Laosia* is nearly basal in the Asian Podostemoideae and geographically adjacent to *Ctenobryum* (Fig. 1, code 8a vs. 9) and *Hydrodiscus* (vs. 8). The three genera with their own histories may have originated or taken refuge in the PKK Area, pending further study.

Hydrobryum is the largest genus with 33 species in Asian Podostemaceae (Koi & Kato, 2019). Nine of the 11 species occurring in the PKK Area are endemic, while the other two species are non-endemic. Ten of the 11 species, together with three other species, form the Lao *Hydrobryum* clade (Koi & Kato, 2019), while the remained *H. vientianense* is far from the clade. In this clade, the species of the PKK Area are divided into five sister pairs, and each species is distinct from its sister species (Table 2). Sister pairs 2 and 3 are sister to each other and so are sister pairs 4 and 5, while sister 1 is sister to *H. nakaiense* Koi & M.Kato occurring outside the PKK Area. The

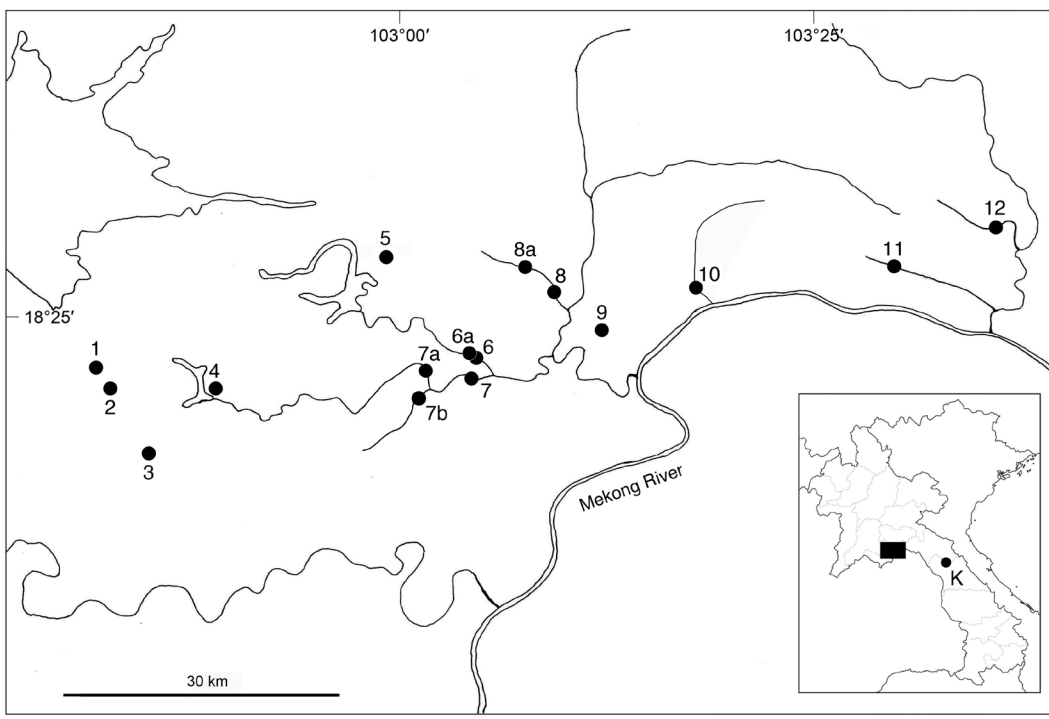

Figure 1. Sites of Podostemaceae in the PKK Area indicated by location codes (Table 1). Site K = NE of Ban Mak Pheuang, N side of Nam Theun River, Khammouane Province, 17°51′47″N, 105°20′02″E.

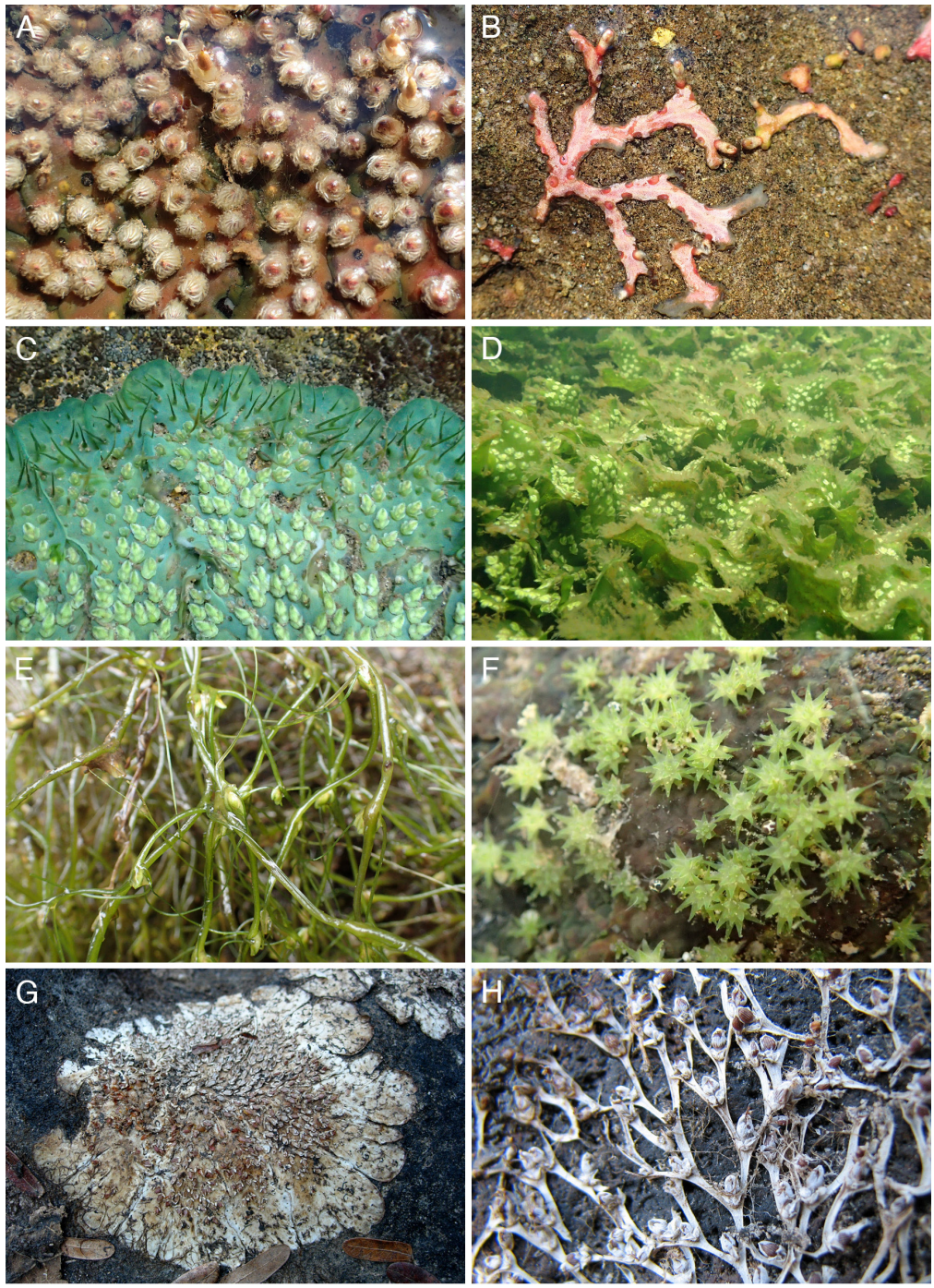

Figure 2. Podostemaceae on riverbed rocks in the PKK Area. A. *Ctenobryum mangkonense* Koi & M.Kato; bract-subtended flower buds scattered on foliose roots. B. *Dalzellia pseudoangustissima* Koi & M.Kato. C. *Hydrobryum clandestinum* Koi & M.Kato; linear leaves and flower buds scattered on foliose roots. D. *H. hapteron* Koi & M.Kato; flower buds scattered on floating foliose roots. E. *H. ramosum* (C.Cusset) Koi & M.Kato; roots bearing flower buds at branching; plants taken out. F. *H. stellatum* Koi & M.Kato; flower buds with radially arranged bracts on foliose roots. G. *H. subcrustaceum* Koi & M.Kato; fruits on desiccated foliose roots. H. *H. subcylindricum* Koi & M.Kato; desiccated root with fruits between branches.

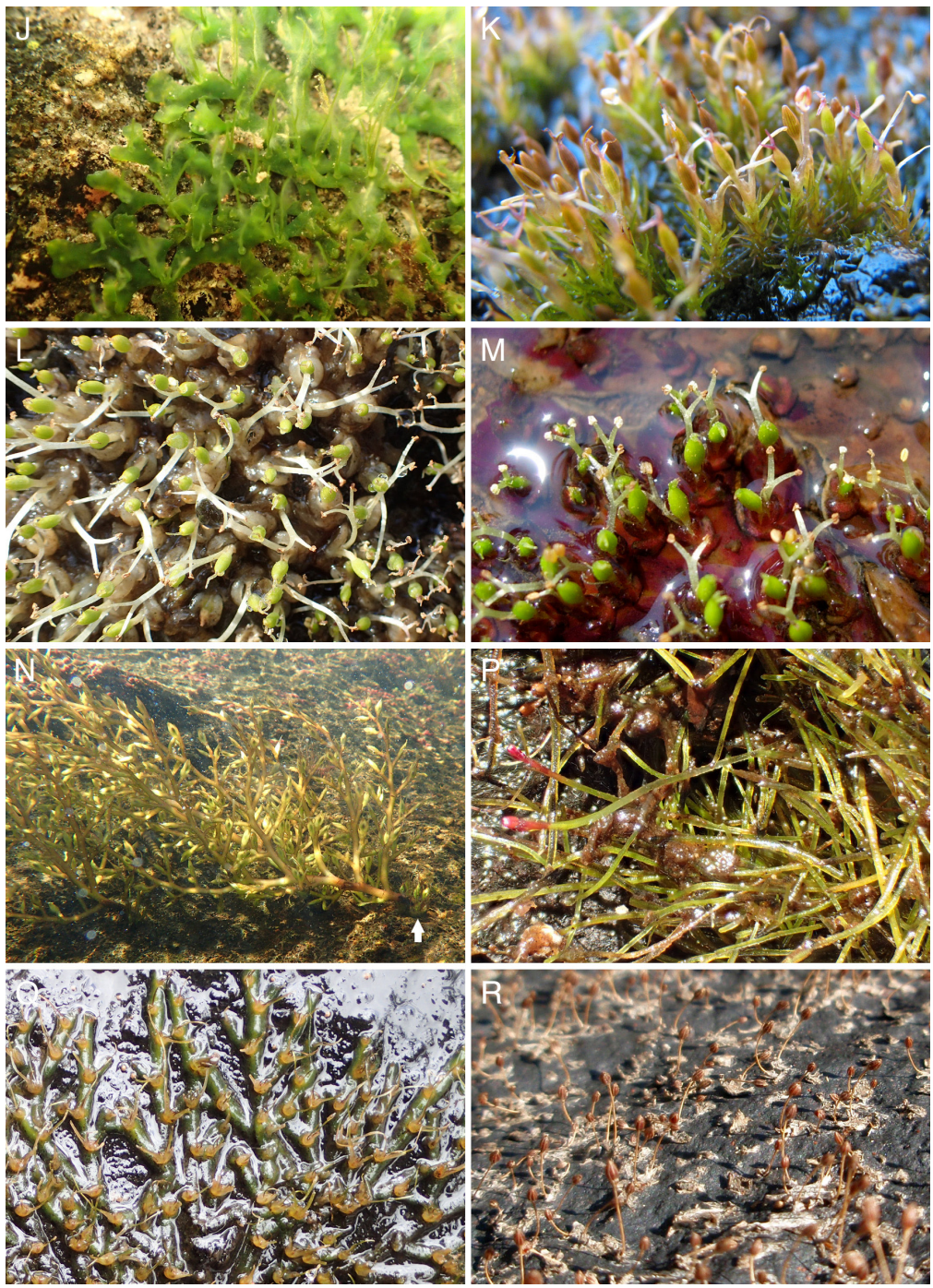

Figure 2.— Continued. J. *Hydrobryum taeniatum* Koi & M.Kato; ribbon-like roots bearing leaves at branching points. K. *H. takakioides* Koi & M.Kato; upright flowering shoots on foliose root. L. *H. verrucosum* Koi & M.Kato; flowers on foliose roots. M. *H. vientianense* (M.Kato & Fukuoka) Koi & M.Kato; flowers on foliose roots. N. *Hydrodiscus koyamae* (M.Kato & Fukuoka) Koi & M.Kato; floating, branched shoot adhered at base (marked with arrow). P. *Laosia ramosa* Koi, Won & M.Kato; cylindrical organs, some of which have terminal flower buds (red); plants taken out. Q. *Polypleurum pluricostatum* Koi & M.Kato; ribbon-like roots with shoots at branching points. R. *P. schmidtianum* Warm.; fruits. Photographed by S. Koi (C, D, F, G, J, M, N), M. Kato (A, B, E, H, L, P–R) and N. Katayama (K).

Table 1. Podostemaceae in Phou Khao Khouay National Park and adjoining areas and their locations. Location codes are mapped in Fig. 1.

Species	Endemism*	Location (code in parentheses)	Latitude/longitude
Ctenobryum mangkonense Koi & M.Kato	E	Tad Mangkone waterfall, elev. 177 m (9)	18°25′58.1″N, 103°12′39.9″E
Dalzellia kailarsenii M.Kato	N[1]	Ban Nam Hyam, 620 m (2)	18°21′02.2″N, 102°42′36.2″E
D. pseudoangustissima Koi & M.Kato	E	Tad Leuk waterfall, 200 m (6)	18°23′42.9″N, 103°04′17.0″E
		1 km from Tad Leuk waterfall, 195 m (6a)	18°24′02.8″N, 103°03′08.4″E
		Tad Yong waterfall, 160 m (7)	18°21′45.8″N, 103°04′50.6″E
		Tad Xai waterfall, 290 m (8)	18°27′18.8″N, 103°08′31.8″E
		Tad Lo waterfall, Ban Si Som Xay, 160 m (10)	18°27′02.9″N, 103°17′48.7″E
Hydrobryum clandestinum Koi & M.Kato	E	waterfall above Tad Xai waterfall, 411 m (8a)	18°28′01.1″N, 103°07′41.2″E
		Tad Heua Hak waterfall, 162 m (11)	18°28′23.8″N, 103°31′20.2″E
H. hapteron Koi & M.Kato	E	rapids above Tad Xai waterfall, 422 m (8a)	18°28′15.5″N, 103°07′23.0″E
		rapids above Tad Xai waterfall, 421 m (8a)	18°28′15.5″N, 103°07′22.9″E
H. ramosum (C.Cusset) Koi & M.Kato	E	Nam Mang 3 Dam, Mt. Phou Khao Khouay, 750 m (4)	18°21′38.0″N, 102°48′26.3″E
		Tad Omong waterfall near Nam Mang 3 Dam, Ban Vanghuea, 750 m (4)	18°21′38.0″N, 102°48′26.3″E
		stream 300 m apart from Nam Mang 3 Dam, Phu Khao Khwai, 720 m (4)	18°21′26.8″N, 102°48′28.6″E
		Phu Khao Khwai (= Phou Khao Khouay)	n/a
		Phu Khao Khwai	n/a
H. stellatum Koi & M.Kato	E	Tad Yong, 164 m (7)	18°21′45.8″N, 103°04′50.4″E
H. subcrustaceum Koi & M.Kato	E	Chaova waterfall, 200 m (1)	18°22′07.9″N, 102°42′13.3″E
		Tad Omong near Nam Mang 3 Dam, Ban Vanghuea, 750 m (4)	18°21′38.0″N, 102°48′26.3″E
		Nam Mang 3 Dam, 750 m (4)	18°21′35.9″N, 102°48′25.3″E
H. subcylindricoides Koi & M.Kato	E	upstream of Tad Xai, 400 m (8a)	18°28′15.5″N, 103°07′23.0″E
H. subcylindricum Koi & M.Kato	E	Tad Leuk waterfall, 200 m (6)	18°23′42.9″N, 103°04′17.0″E
		Tad Yong waterfall, 164 m (7)	18°21′45.8″N, 103°04′50.4″E
		waterfall above Tad Yong waterfall (7a)	18°22′03.9″N, 103°04′03.9″E
		Tad Xai waterfall, 300 m (8)	18°27′18.8″N, 103°08′31.8″E
		Tad Xai waterfall, 300 m (8)	18°27′07.0″N, 103°08′39.5″E
H. taeniatum Koi & M.Kato	E	Tad Leuk waterfall, 200 m (6)	18°23′42.9″N, 103°04′17.0″E
		Rapids 1 km above Tad Leuk waterfall, 208 m (6a)	18°23′58.0″N, 103°03′54.4″E
		Tad Yong waterfall, 164 m (7)	18°21′45.8″N, 103°04′50.4″E
		waterfall above Tad Yong waterfall, 202 m (7a)	18°22′03.9″N, 103°04′03.9″E

Table 1. continued.

Species	Endemism*	Location (code in parentheses)	Latitude/longitude
		tributary above Tad Yong waterfall, 198 m (7b)	18°21′49.4″N, 103°03′50.7″E
		Tad Lo waterfall, Ban Si Som Xay, 160 m (10)	18°27′02.9″N, 103°17′48.7″E
		Tad Nampa waterfall, Ban Nampa, 163 m (12)	18°30′47.7″N, 103°36′26.8″E
Hydrobryum takakioides Koi & M.Kato	E	Tad Xai waterfall, 300 m (8)	18°27′18.8″N, 103°08′31.8″E
H. verrucosum Koi & M.Kato	N[2]	Tad Leuk waterfall, 200 m (6)	18°23′42.9″N, 103°04′17.0″E
		rapids 1 km above Tad Leuk waterfall, 208 m (6a)	18°23′58.0″N, 103°03′54.4″E
		Tad Yong waterfall, 164 m (7)	18°21′45.8″N, 103°04′50.4″E
		waterfall above Tad Yong waterfall, 202 m (7a)	18°22′03.9″N, 103°04′03.9″E
		Tad Xai waterfall, 300 m (8)	18°27′07.0″N, 103°08′39.5″E
		Tad Xai waterfall, 300 m (8)	18°27′18.8″N, 103°08′31.8″E
		waterfall above Tad Xai waterfall, 411 m (8a)	18°28′01.1″N, 103°07′41.2″E
		Tad Nampa waterfall, Ban Nampa, 163 m (12)	18°30′47.7″N, 103°36′26.8″E
H. vientianense (M.Kato & Fukuoka) Koi & M.Kato	N[3]	Tad Chan Thevoda waterfall, 200 m (3)	18°17′52.4″N, 102°45′10.6″E
Hydrodiscus koyamae (M.Kato & Fukuoka) Koi & M.Kato	E	Tad Leuk waterfall, 200 m (6)	18°23′42.9″N, 103°04′17.0″E
		Tad Yong waterfall, 164 m (7)	18°21′45.8″N, 103°04′50.4″E
		waterfalls above Tad Yong waterfall, 202 m (7a)	18°22′03.9″N, 103°04′03.9″E
		Tad Xai waterfall, 300 m (8)	18°27′07.0″N, 103°08′39.5″E
		Tad Xai waterfall, 300 m (8)	18°27′18.8″N, 103°08′31.8″E
		Tad Nampa waterfall, Ban Nampa, 163 m (12)	18°30′47.7″N, 103°36′26.8″E
Laosia ramosa Koi, Won & M.Kato	E	Pha Xet waterfall, 637 m (5)	18°30′10.3″N, 102°58′03.8″E
		Pha Xet waterfall, 616 m (5)	18°30′10.7″N, 102°58′01.9″E
		tributary above Tad Xai waterfall, 475 m (8a)	18°28′27.5″N, 103°07′40.2″E
		tributary of Tad Xai waterfall, 406 m (8a)	18°28′15.5″N, 103°07′23.0″E
Polypleurum pluricostatum Koi & M.Kato	N[4]	Nam Mang 3 Dam, 700 m (4)	18°21′26.8″N, 102°48′28.6″E
		Tad Omong near Nam Mang 3 Dam, Ban Vanghuea, 750 m (4)	18°21′38.0″N, 102°48′26.3″E
P. schmidtianum Warm.	N[5]	Tad Nampa waterfall, Ban Nampa, 163 m (12)	18°30′47.7″N, 103°36′26.8″E

* E=endemic to PKK area, N=non-endemic.

[1–5] Additional areas: [1] North-Eastern Thailand; [2] site K in Khammouane Province, Central Laos; [3] Central Laos and North-Eastern Thailand; [4] North-Eastern Thailand; [5] Cambodia and Thailand.

distributions indicate that the species belonging to each sister pair, except those of sister 3, are allopatric and separated by short distances (Fig. 1, Table 2). It may suggest that the speciation is usually allopatric producing neo-endemics in spite of small geographical separation. In conclusion, the PKK Area is a likely centre for the origin of the neoendemics, although it is not excluded that the PKK Area might be a refugium for some of them. The centre of distribution might have continued to exist for a long time, because it is consistent with the possibilities that the endemic *Ctenobryum* and *Hydrodiscus* have existed in the PKK Area since the separation from *Hydrobryum* and allied genera (Koi & Kato, 2019) and that *Laosia* is paleoendemic since the separation from Southeast-East Asian Podostemaceae subfamily Podostemoideae (Koi *et al.*, 2019).

While most species of *Hydrobryum* are foliose-rooted, four PKK Area-endemic species are sub-cylindrical/ribbon-like-rooted and sister to individual foliose-rooted species endemic to the PKK Area (Table 2). That is, *H. subcylindricoides* Koi & M.Kato is sister to *H. subcrustaceum* Koi & M.Kato,

Table 2. Characters of species of the Lao *Hydrobryum* clade, with distribution and phylogenetic relationship.

Species	*H. austrolaoticum*	*H. somranii*	*H. nakaiense*	*H. subcylindricoides*	*H. subcrustaceum*	*H. takakioides*	*H. stellatum*	*H. subcylindricum*	*H. tae-niatum*	*H. ramosum*	*H. hapteron*	*H. clandestinum*	*H. verrucosum*
Distribution*	non-PKK	non-PKK	non-PKK	8a	1, 4	8	7	6, 7, 7a, 8	6, 6a, 7a, 7b, 10, 12	4	8a	8a,11	6, 6a, 7, 7a, 8, 8a, 12, K
Phylogeny**	—	—	—	sister 1		sister 2		sister 3		sister 4		sister 5	
Root	1	1	1	3	1	1	1	3	2	3	1	1	1
Holdfast	1	1	1	1	1	1	1	1	1	2	2	1	3
Flowering shoot	1	1	1	1	1	2	1	1	1	1	1	1	1
Bract (number)	1	1	1	1	1	2	2	1	1	1	1	1	1
Bract (form)	1	1	1	1	1	2	2	1	1	1	1	1	1
Bract (taxis)	1	1	1	1	1	2	2	1	1	1	1	1	1
Spathella	1	1	1	1	1	1	1	2	1	1	1	2	1
Stamen	1	2	2	1	2	1	1/2	1	2	2	2	1	2
Ovary locule	1	2	2	2	2	2	1	2	2	2	2	1	2
Rib on capsule	2	2	2	1	2	2	2	2	2	2	2	2	2

Abbreviations of character states. Root: code 1 = foliose, 2 = ribbon-like, 3 = subcylindrical. Holdfast: 1 = discoid, 2 = cylindrical, 3 = warty. Flowering shoot (length): 1 = ≤3 mm, 2 = 7–14 mm. Bract (number): 1 = 2–6, 2 = 10–40. Bract (form): 1 = ovate, 2 = linear. Bract (taxis): 1 = 2-rowed, 2 = spiral/irregular. Spathella: 1 = caducous, 2 = persistent. Stamen (number): 1 = 1, 2 = 2 on common andropod. Ovary locule (number): 1 = 1 with 2 incompletely separated locules, 2 = 2. Range of ribs on capsule (number): 1 = 10–12, 2 = 12–18.

* non-PKK= non-PKK area; 1–12, K = site codes in Table 1 and Fig. 1.

** Sister 1 is sister to *H. nakaiense* Koi & M.Kato, sister 2 is sister to sister 3, and sister 4 is sister to sister 5. *H. austrolaoticum* Koi & M.Kato is sister to the rest of the Lao clade. *H. somranii* M.Kato is allied to a group of sister 1 and *H. nakaiense* Koi & M.Kato and to a group of sisters 2 and 3. Data from Koi & Kato (2019).

both in group 1, *H. subcylindricum* Koi & M.Kato/*H. taeniatum* Koi & M.Kato of sister 3 are sister to *H. takakioides* Koi & M.Kato/*H. stellatum* Koi & M.Kato of sister 2, and *H. ramosum* (C.Cusset) Koi & M.Kato is sister to *H. hapteron* Koi & M.Kato, both in sister 4. The evolution of the subcylindrical/ribbon-like root from the foliose root is recurrent in three lineages and opposite to the early evolution of the foliose root from the ribbon-like root at the divergence of the *Hydrobryum* lineage from the Cladopus lineage (Koi & Kato, 2020). The latter direction of evolution happened in other South Asian-Southeast Asian lineages and African genera, providing other cases of the recurrent opposite evolution (Koi & Kato, 2020). The subcylindrical/ribbon-like- and foliose-rooted species are sympatric, and occasionally even on the same rock, in the PKK Area, indicating equivalent adaptability of the two root forms. Based on the recurrent two-way evolution and equivalent adaptability, Koi & Kato (2020) interpreted the evolution of the root form as non-adaptive or neutral, although it is apt to be regarded as adaptive.

Hydrobryum subcylindricum and *H. taeniatum* are reciprocally sister and polyphyletic (Koi & Kato, 2012); the polyphyly will be tested by our ongoing study. The polyphyletic species, if accepted, are recorded for the first time in Podostemaceae and, to our knowledge, rare in other plants. Most congeners are monophyletic and *H. japonicum* Imamura is paraphyletic (Kato *et al.*, 2019). In light of the phylogenetic species concept (Avise, 2000; Rosenberg, 2003), the polyphyletic *H. subcylindricum* and *H. taeniatum* can be interpreted to represent the first stage of species transition.

In conclusion, the Podostemaceae of the PKK Area are remarkably diverse and include many endemic genera and species. Furthermore, the endemic species may be in-situ productions by notable evolution involving allopatric speciation with little geographical and ecological isolation, phylogenetic-species transition, saltatory evolution, and non-adaptive evolution. The PKK Area inhabited by these plants is evaluated as a micro-scale hotspot of global importance for conservation in terms of the Podostemaceae taxa. The cause of the high endemism in the small area remains to be determined.

ACKNOWLEDGEMENTS

We thank Thawatchai Wongprasert and Petcharat Werukamkul for help in the field work, and two anonymous reviewers and editors for the comments on the manuscript. This study was supported by the KAKENHI Grants Nos. 19255007 and 25291091 to M.K.

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