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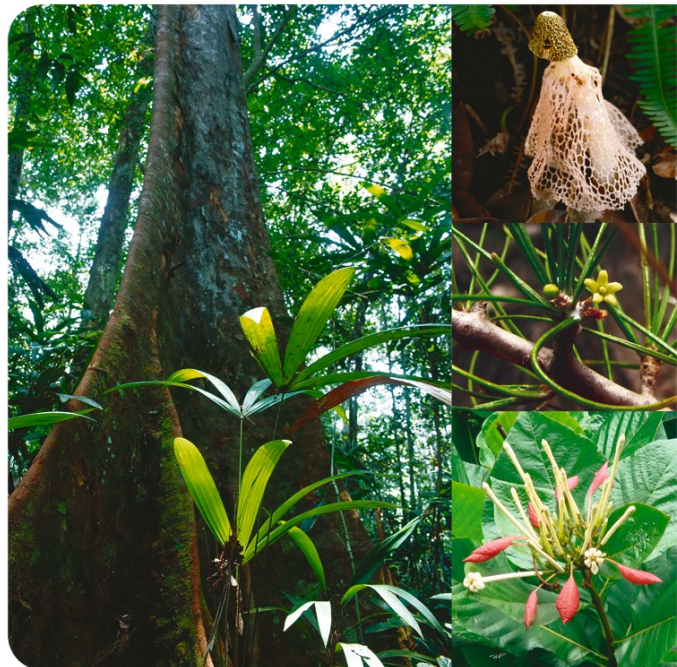
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A taxonomic study of Podostemaceae subfamily Podostemoideae of Laos with phylogenetic analyses of *Cladopus*, *Paracladopus* and *Polypleurum*

Satoshi Koi^{1,2} & Masahiro Kato¹

Summary. The Podostemaceae of Laos are much less understood than those of adjacent Thailand. Comparative morphology using new materials, together with the latest molecular phylogenetic studies, have revealed a high diversity in subfamily Podostemoideae in Laos. This subfamily comprises five genera and 15 species. The genus *Hydrobryum* Endl. is enlarged, and found to be remarkably diverse in root and shoot morphology. We describe two species, *H. subcylindricum* sp. nov. and *H. taeniatum* sp. nov., with subcylindrical and ribbon-like roots, respectively; *H. austrolaoticum* sp. nov., *H. verrucosum* sp. nov. and *H. subcrustaceum* sp. nov. with crustose roots, and *H. takakioides* sp. nov. with crustose roots and elongate shoots. *Diplobryum* C. Cusset, comprising four species and characterised solely by the nearly 20-ribbed capsule, is polyphyletic. Two Lao and a Vietnamese species of *Diplobryum* are transferred to *Hydrobryum*: *H. ramosum* (C. Cusset) Koi & M. Kato comb. nov., with floating subcylindrical roots and anchoring disk-like bases, and *H. vientianense* (M. Kato & Fukuoka) Koi & M. Kato comb. nov. and *H. minutale* (C. Cusset) Koi & M. Kato comb. nov. with crustose roots. The rootless *D. koyamae* M. Kato & Fukuoka was recently combined as *Hydrodiscus koyamae* (M. Kato & Fukuoka) Koi & M. Kato. *Cladopus* (sect. *Griffithella*) *pierrei* (Lecomte) C. Cusset is not segregated even at a sectional rank. We also describe *Polypleurum pluricostatum* sp. nov., and add *Hydrobryum tardhuangense* M. Kato, *Paracladopus Chiangmaiensis* M. Kato and *Polypleurum schmidtianum* Warm. as new records to Laos, and *Polypleurum wallichii* (R. Br. ex Griff.) Warm. from new localities in Laos.

Key Words. Flora, *matK*, taxonomy, Thailand.

Introduction

The Podostemaceae is a family of unusual aquatic angiosperms comprising c. 280 species classified in 49 genera. The family, commonly known as river-weeds, is found in rapids and waterfalls in the tropics and subtropics: the habitats are quite similar across the world. Vegetative plants grow submerged in turbulent water, firmly adhering on rock surfaces during the rainy season. When the water level lowers during the dry season the plants become exposed, producing flower and fruit, before finally desiccating. Therefore the plants are forcibly annual. The vegetative plants are alga-, liverwort- or moss-like as adaptations to such an environment. The flowers are reduced and simple, consisting of a few filiform or lobed tepals, 1–3 stamens (but multiple in American species), and a single, 2–3-carpellate pistil.

The earliest floristic treatment of Lao Podostemaceae was made by Cusset (1973a, b), who enumerated three species, *Cladopus pierrei* (Lecomte) C. Cusset (Podostemoideae), *Dalzellia carinata* (Lecomte) C. Cusset, and *Da. diversifolia* (Lecomte) C. Cusset (Tristichoideae) (the subfamilies were treated as

families). Later, *Diplobryum ramosum* C. Cusset was added (Cusset 1992). Kato & Fukuoka (2002) described two more species of *Diplobryum* C. Cusset, *Di. vientianense* M. Kato & Fukuoka and *Di. koyamae* M. Kato & Fukuoka, although they doubted the monophyly of the genus, and added a new record of *Polypleurum wallichii* (R. Br. ex Griff.) Warm. *Dalzellia carinata* and *Da. diversifolia* were transferred to the new genus *Cussetia* M. Kato (Kato 2006a). As a result, three genera and five species of Podostemoideae and one genus and two species of Tristichoideae have so far been recognised.

Diplobryum is an enigmatic genus. It was established by Cusset (1972) for *Di. minutale* C. Cusset from southern Vietnam. The genus was characterised by the crustose root, the capitate stigma, the 20-ribbed capsule, the ovary-stalk protruding beyond the spathe and bracts, and the ellipsoidal or lenticular, ribbed seed (Cusset 1972, 1973a). *Di. ramosum* is distinct from *Di. minutale* in its cylindrical, repeatedly branched roots and linear, elongate stigmas (Cusset 1992). *Di. vientianense*, like *Di. minutale*, has crustose

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roots bearing flowers scattered on the dorsal surface, whereas *Di. koyamae*, like *Di. ramosum*, has floriferous, ramified axes (the homology of which to the root or shoot was uncertain) (Kato & Fukuoka 2002). Thus the enlarged genus *Diplobryum* was poorly defined by a single character, i.e. the 20-ribbed capsule, and is remarkably heterogenous. Very recently Koi & Kato (2010) proposed a new genus *Hydrodiscus* Koi & M. Kato for *Di. koyamae*, based on molecular phylogenetic relationships and evidence of seedling and shoot development.

Investigation of Podostemaceae in Laos was motivated by recent progress of taxonomy of the family in adjacent Thailand. For Thai Podostemaceae, Cusset (1973a, b; 1992) and Cusset & Cusset (1988) have recorded in total seven genera and 10 species. In floristic studies of the family mostly based on recent collections, Kato (2004, 2006a), Kato *et al.* (2004), Koi *et al.* (2008) and Kato & Koi (2009) enumerated 10 genera and 42 species, indicating that Thailand is a centre of diversity of the family in Asia. This remarkably enlarged number of taxa implies that the Podostemaceae of Laos, northeast of Thailand, are potentially more diverse than we assumed. It will not be surprising if more species are discovered by future explorations.

This paper describes a new and revised taxonomy of the subfamily Podostemoideae of Laos, based on comparative morphology using new materials, along with the latest molecular phylogenetic relationships (Koi & Kato 2010) and those revealed in this study. Due to insufficient field observations and lack of collections from Laos, the conservation assessments given below are very preliminary. The habitat is restricted to exposed rapids and waterfalls, where populations are patchy, and is still undisturbed in most areas. Generally the Lao species are near threatened (NT) according to IUCN conservation ratings. Podostemaceae will be threatened by future water pollution and dam construction.

Materials and methods

Materials were collected from central and southern Laos (according to administrative divisions), and all vouchers are deposited in the Herbarium (TNS), Department of Botany, National Museum of Nature and Science (Tsukuba); Forest Herbarium (BKF), Department of National Parks, Wildlife and Plant Conservation (Bangkok); and National University of Laos Herbarium. These herbaria are not listed in the specimen citations; locations of specimens from other herbaria are given.

For comparative morphology, materials were fixed with FAA (formaldehyde:acetic acid:50% ethyl alcohol = 5:5:90). We also examined specimens deposited in University of Copenhagen Herbarium (C), Royal Botanic Garden Edinburgh Herbarium (E), Herbari-

um of Royal Botanic Gardens, Kew (K), National Herbarium of the Netherlands (L), Herbarium of National Museum of Natural History, Paris (P), and University of Tokyo Herbarium (TI).

Materials for phylogenetic analysis are listed in the Appendix. Analysis was performed using chloroplast *matK* sequences. The methods of DNA extraction, sequencing and phylogenetic analyses are described in Koi & Kato (2010). For the maximum likelihood (ML) and Bayesian analyses, the program Modeltest (version 2.3; Posada & Crandall 1998) and the Akaike Information Criterion (AIC; Akaike 1974) were used to determine the best DNA substitution model for the present dataset; the General Time Reversible model with proportion of invariable sites and an alpha shape parameter for the gamma distribution (GTR+I+G) was selected. In the analyses of the *Cladopus-Hydrobryum* clade, the following parameter values were used: nucleotide frequencies were A = 0.3265, C = 0.1477, G = 0.1251, T = 0.4007; the substitution rate matrix was A to C = 1.2814, A to G = 1.1151, A to T = 0.2374, C to G = 0.5374, C to T = 0.9087, G to T = 1.0000; the proportion of invariable sites was 0.2753; and the gamma distribution shape parameter was 0.9412. In the analyses of the *Polypleurum* clade, the following parameter values were used: nucleotide frequencies were A = 0.3318, C = 0.1458, G = 0.1366, T = 0.3857; the substitution rate matrix was A to C = 0.8628, A to G = 1.0083, A to T = 0.1104, C to G = 0.3656, C to T = 0.9279, G to T = 1.0000; the proportion of invariable sites was 0.4696; and the gamma distribution shape parameter was 1.0854. Heuristic searches were conducted with 100 random addition replicates involving nearest-neighbor-interchange (NNI) branch swapping. Bootstrap values were calculated for 100 replicates with 10 random addition replicates involving NNI branch swapping. In maximum parsimony (MP) analyses, bootstrap values were calculated for 1000 replicates with 10 random addition replicates (time limit of 10 minutes was imposed for each addition replicate in the analysis of the *Cladopus-Hydrobryum* clade) involving tree-bisection-reconnection (TBR) branch swapping. In the Bayesian analysis, the GTR model+I+G was selected and Markov chain Monte Carlo (MCMC) iterations with four chains were conducted for 2,000,000 generations, sampling every 100 generations. The first 5,000 trees were discarded as burn-in, and the remaining 15,000 trees were used to calculate a 50% majority-rule tree and to determine the posterior probabilities for branches. *Polypleurum stylosum* (Wight) J. B. Hall, *Zeylanidium lichenoides* (Kurz) Engl. and *Z. subulatum* (Gardner) C. Cusset of subfamily Podostemoideae were treated as outgroups in the analysis of the *Cladopus-Hydrobryum* clade, and two samples of *Z. subulatum* were the outgroup in the analysis of the *Polypleurum* clade (Kita & Kato 2001, 2004; M. Kato, unpubl. data).

Results and discussion

Morphology

The results of the comparative morphology study are shown in the Key, Table 1, and the descriptions of taxa below.

Phylogeny

Koi & Kato (2010) performed an ML phylogenetic analysis of the *matK* gene for *Cladopus* H. A. Möller and *Paracladopus* M. Kato, and a monophyletic clade of the two genera was illustrated as a triangle with no species names given on the tree. In the present tree (Fig. 1A), deduced using added materials and the same method, the *Cladopus pierrei* clade includes *C. doianus* (Koidz.) Kōriba, and the two form a clade with *C. fukienensis* (H. C. Chao) H. C. Chao and *C. austrosinensis* M. Kato & Y. Kita, the latter three of which are distributed in China and Japan. *C. taiensis* C. Cusset and *C. fallax* C. Cusset of Thailand form another clade with Indonesian and Australian species. The Lao and Thai plants of *Paracladopus Chiangmaiensis* M. Kato form a clade which is sister to *P. Chanthaburiensis* Koi & M. Kato.

The present phylogenetic analysis for *Hydrobryum* Endl. and related genera, consistent with the latest results (Koi & Kato 2010), indicates monophyly of *Hydrodiscus koyamae*, *Diplobryum* (= *Hydrobryum*) *vientianense*, *D.* (= *H.*) *ramosum*, and some other crustose-, ribbon-like or subcylindrical-rooted species of Laos, along with *Hanseniella* C. Cusset, *Hydrobryum*, and *Thawatchaia* M. Kato, Koi & Y. Kita, all with crustose roots (Fig. 1A, B). *Hydrodiscus koyamae* is basal in this clade though the monophyly of the other related species is supported with a relatively low bootstrap value. *Diplobryum* (= *Hydrobryum*) *vientianense* of Laos and Thailand forms a clade with *H. loeicum* M. Kato of NE Thailand within the *Hydrobryum* clade. *Diplobryum* (= *Hydrobryum*) *ramosum* and the remaining Lao species of *Hydrobryum*, except *H. tardhuangense* M. Kato, with various root morphologies, form another clade with the crustose-rooted *H. somranii* M. Kato of NE Thailand. These species are described as new below.

The phylogenetic analysis does not support the separation of the genera *Diplobryum* and *Hydrobryum* by Cusset (1972, 1992) and Kato & Fukuoka (2002), and the currently accepted definition of the genus *Hydrobryum* (Cusset 1992; Kato 2004) (Fig. 1B). Many characters shared by *D. vientianense* and Vietnamese *D. minutale*, type of the genus, suggest that *D. minutale* is also assignable to *Hydrobryum*. *D. ramosum* and some other species, like *Cladopus* and *Polypleurum* (Taylor ex Tul.) Warm., have non-crustose roots, but they are referable to *Hydrobryum*. Because *Hydrobryum* had conventionally been characterised by a few characters such as the crustose roots and more than 8-ribbed,

flattened capsules, the taxonomic definition of this polymorphic genus revealed here is amended below.

A phylogenetic analysis of *Polypleurum* shows that it is divided into two subclades (Fig. 2). One subclade includes *P. pluricostatum* sp. nov. and, except basal *P. longistylosum* M. Kato, has roots with tufts of leaves borne exclusively at sinuses of root branches (Kato 2006a). The other subclade includes *P. schmidtianum* Warm. and *P. wallichii*, and, like *P. longistylosum*, is characterised by the root with tufts of leaves borne on the flank between root branches.

The trees indicate non-monophyly of some species. *Cladopus pierrei* excluding East Asian *C. doianus*, *Polypleurum pluricostatum* excluding Thai *P. longicaule* M. Kato, and extra-Lao *Hydrobryum japonicum* Imamura excluding Japanese *Hy. floribundum* Koidz. are paraphyletic species. In MP analysis, however, *P. pluricostatum* is monophyletic (data not shown). *Hy. taeniatum* sp. nov. and *H. subcylindricum* sp. nov. are polyphyletic to each other. We accept morphologically recognisable, phylogenetically paraphyletic species in Podostemaceae. In this torrenticolous aquatic family, conspecific populations are isolated in sparse habitats, and most species are distributed in single rivers or in a few isolated rivers (Kato 2006a). It is likely that progenitor species can maintain paraphyletic relationships of populations after progeny species speciated from the colonisers of the progenitors, and progenitor populations are morphologically more similar to each other than to progeny species. Our treatment of paraphyletic species is based on this assumption, which should be verified by close examination.

The ovary is 2- or less often 1-locular in *Hydrobryum* (Table 1). It is 2-locular in the basal *Hydrodiscus*, *Hanseniella* and *Thawatchaia*, and also in most American and other Asian Podostemoideae (Kato 2004, 2006a; Ghogue *et al.* 2009). Therefore the 1-locular ovary is an apomorphic character state. The 1-locular ovary has 2-surfaced placentas with reduced margins, suggesting an early cessation in growth of the septum during ovary development, as implied for African *Djinga felicis* C. Cusset by Ghogue *et al.* (2009). The phylogeny suggests that the reduction of locules happened two or three times in *Hydrobryum*, and in the former case, reversal to the 2-locular ovary happened in *Hy. ramosum* comb. nov. and *Hy. verrucosum* sp. nov. A similar infrageneric reduction occurred in extra-Asian clades, for example, in African *Saxicolella* Engl. (Ameka *et al.* 2002).

The stamens are double with a common andropod in the majority of the *Hydrobryum* clade or single in five species of *Hydrobryum* (Table 1). Because the two stamens are plesiomorphic in the clade, the single stamens are autoapomorphic for the remotely related species. The stamens are usually single or rarely double in *Cladopus* and *Polypleurum*. The two stamens are auto-apomorphic in these genera.

Table 1 Comparison of characters among species of *Hydrodiscus*, *Hanseniella*, *Thawatchaia* and *Hydrobryum* in Southeast Asia. **koyama** = *Hydrodiscus koyamae*; hetero = *Hanseniella heterophylla*; smiti = *Ha. smitinandii*; triloba = *Thawatchaia trilobata*; bifolia = *Hydrobryum bifoliatum*; kaengs = *Hy. kaengsophense*; tardh = *Hy. tardhuangense*; griffith = *Hy. griffithii*; loei = *Hy. loeicum*; somran = *Hy. somranii*; chiang = *Hy. chiangmaiense*; japon = *Hy. japonicum*; khaoya = *Hy. micrantherum*; phetch = *Hy. phetchabunense*; vient = *Hy. vientianense*; minut = *Hy. minutale*; austro = *Hy. australoticum*; verruc = *Hy. verrucosum*; subcrus = *Hy. subcrustaceum*; takak = *Hy. takakioides*; taeni = *Hy. taeniatum*; subcyl = *Hy. subcylindricum*; ramos = *Hy. ramosum*. Lao species are shown in bold face; *Hy. tardhuangense* and *Hy. vientianense* are distributed also in Thailand.

Character	koyama	hetero	smiti	triloba	bifolia	kaengs	tardh	griffith	loeii	somran	chiang	japon
Root*1	absent	crust	crust	crust	crust	crust	crust	crust	crust	crust	crust	crust
Flowering shoot*2	straight	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect
Flower	straight	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect	erect
Ranks of bracts	2	4	4	2	2	2	2	2	2	2	2	2
No. of bracts	8-15	≤24	≤28	8-12	2-3	4-6	2-3	5-6	4-6	2-4	4	4-5
Bract conformity*3	uniform	dimorph	dimorph	uniform	uniform	uniform	uniform	uniform	uniform	uniform	uniform	uniform
Shape of bract	simple	bilobed/simple	bilobed/simple	trilobed	simple	simple	simple	simple	simple	simple	simple	simple
Bract tip*4	acumin	obtus	obtus	acute	acumin	acumin to linear	acute	obtus	obtus	obtus	obtus	obtus
Spathella*5	irr	irr	irr	irr	irr	irr	longi	irr	irr	longi	irr	irr
Stamens	2	2	2	2	2	2	2	2	2	2	2	2
Ovary locule	2	2	2	2	2	2	2	2	2	1	2	2
No. of ovules*6	20-41	4-6	4-6	7-9	17-25	16-18	13-25	22-29	4-7	6-12	12-20	11-15
Ovule disposition*7	M+C	M	M	M	M+C	M+C	M	M+C	M	M	M+C	M
Length of stigma	unequal	equal	equal	equal	unequal	unequal	equal	equal	equal	equal	equal	equal
Stigma*8	entire	entire	entire	entire	entire	entire	entire	entire	entire	entire	entire	entire
No. of capsule ribs	18-20	12-16	8	8-10	14-20	12-14	15-16	12-14	16-20	12-14	12-14	12-14
Character	khaoya	micran	phetch	vient	minut	austro	verruc	subcrus	takak	taeni	subcyl	ramos
Root*1	crust	crust	crust	crust	crust	crust	crust	crust	crust	ribbon	narrow	subcylin
Flowering shoot*2	appress	appress	appress	appress	appress	appress	appress	appress	elongate	appress	ribbon	straight
Flower	oblique	oblique	oblique	erect	oblique	oblique	erect	oblique	erect	oblique	oblique	straight
Ranks of bracts	2	2	2	2	2	2	2	2	6-7	2	2	2
No. of bracts	2-3	2-4	2-4	3-6	2	2-6	3-6	2-4	22-34	2-4	2-4	4-6
Bract conformity*3	uniform	uniform	uniform	uniform	uniform	uniform	uniform	uniform	uniform	uniform	uniform	uniform
Shape of bract	simple	simple	simple	simple	simple	simple	simple	simple	simple	simple	simple	simple
Bract tip*4	obtus	obtus	obtus	obtus	obtus	obtus	obtus	obtus	subulate	obtus	obtus	linear
Spathella*5	irr	irr	irr	longi	longi	longi	longi	irr	irr	irr	irr	longi
Stamens	1	1	2	2	2	1	2	2	1	2	1	2
Ovary locule	2	2	2	2	2	1	2	1	1	1	1	2
No. of ovules*6	17-23	9-13*9	4-8	8-27	25-28	13-67	17-67	18-36	20-45	20-27	20-49	30-61
Ovule disposition*7	M	M	M	M+C	M+C	M+C	M+C	M	M+C	M	M	M+C
Length of stigma	equal	equal	equal	equal	equal	equal	equal	equal	equal	equal	equal	equal
Stigma*8	entire	entire	entire	entire	entire	entire	entire	entire	entire	entire	entire	entire
No. of capsule ribs	12-14	12-14	16-20	12-18	20	14-16	15-18	12-16	15-17	16-17	16-20	16-18

*1 crust = crustaceous; ribbon = narrow ribbon-like, narrow ribbon = narrow ribbon-like, subcylin = subcylindrical; *2 appress = appressed; *3 dimorph = dimorphic; *4 acumin = acuminate; *5 irr = ruptured irregularly near apex; longi = longitudinally split; papil = papillate; *6 number of ovules per locule, but per placental face in a 1-locular ovary; *7 M = on marginal surface of septum, M + C = on septum surface except in lower central area; *8 subentire = subentire; *9 top = var. *micrantherum*, bottom = var. *crassum*

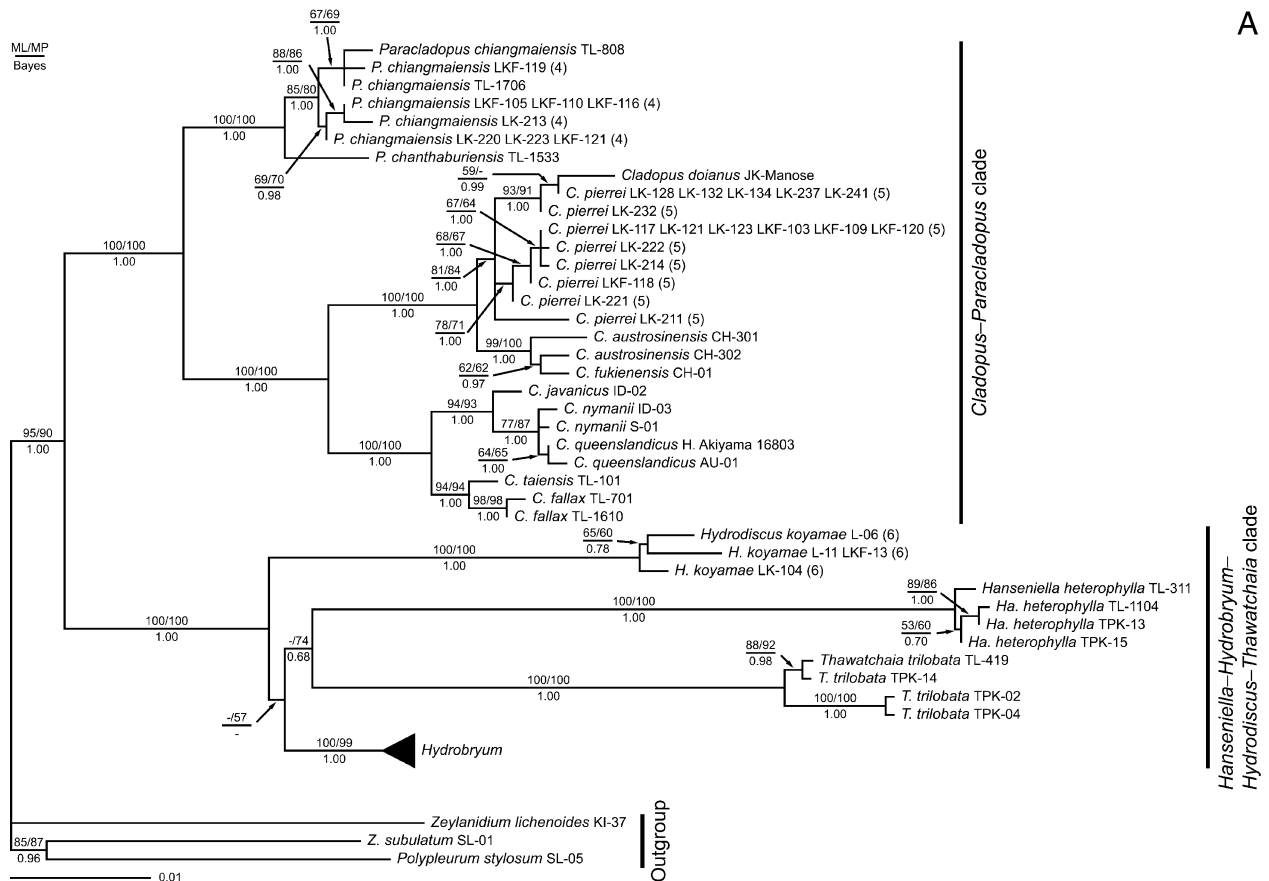


Fig. 1. ML phylogenetic trees of *matK* of *Cladopus*, *Hanseniella*, *Hydrodiscus*, *Paracladopus* and *Thawatchaia* clades (*Hydrobryum* clade is shown as triangle) (A) and *Hydrobryum* clade (B, opposite). Numbers above and below branches indicate bootstrap supports (>50 %) of ML (left) and MP (right), and posterior probabilities (>0.50) of Bayesian analyses, respectively. *Polypleurum* and *Zeylanidium* species are treated as outgroups. Numbers in parentheses following species names are species numbers used in this paper.

Floristic comparison

Based on molecular and morphological evidence, we recognise *Cladopus* (1 sp.), *Hydrobryum* (9 spp.), *Hydrodiscus* (1 sp.), *Paracladopus* (1 sp.), and *Polypleurum* (3 spp.) in the subfamily Podostemoideae. In Laos, another subfamily also occurs, Tristichioideae, which comprises *Cussetia* (2 spp.), *Datzellia* (a few species) and *Terniopsis* H. C. Chao (several species) (S. Koi & M. Kato, unpubl. data), which requires further study. Among the taxa, *Paracladopus* had been regarded as endemic to Thailand (Kato 2006a; Koi *et al.* 2008), but here we record *P. chiangmaiensis* from Laos. *Hydrodiscus* is endemic to Laos and phylogenetically sister to all other members of the *Hydrobryum* group. *Hydrobryum* species with subcylindrical to ribbon-like roots and with prominent shoots are also restricted to Laos, so the Lao *Hydrobryum* group is remarkably diverse. It is possible that there are still scientifically unknown species because of poor collections made to date.

Six species from three genera, *Cladopus*, *Hydrobryum* and *Terniopsis*, occur in China, while six species of *Cladopus* and *Hydrobryum* are found in Japan (Kato &

Kita 2003; Kita & Kato 2004; Kato 2008). A few species are distributed in adjacent Cambodia and Vietnam. Podostemaceae of Myanmar (Burma) perhaps includes three species of three genera, *Hydrobryum*, *Polypleurum* and *Zeylanidium* (Tul.) Engl. (Cusset 1992; Kato 2006b; Tanaka *et al.* 2006). Northern India, Nepal and Bhutan are inhabited by three species of three genera, *Hydrobryum*, *Polypleurum* and *Zeylanidium* (Cusset 1992; Kato 2006b; Kato & Koi 2009). Ten genera and more than 24 species occur in southern India and Sri Lanka (Cusset & Cusset 1988; Cusset 1992; Mathew & Satheesh 1997), which remain to be reinvestigated. Only a single species, *Terniopsis malayana* (J. Dransf. & Whitmore) M. Kato, is distributed in Malaysia (peninsular), two species are found in Indonesia (*Cladopus javanicus* M. Kato & Hambali and *C. nymanii* H. A. Möller), one species occurs in Papua New Guinea (*C. queenslandicus* (Domin) C. D. K. Cook & Rutish.), and in N Australia there are two species of two genera (*C. queenslandicus* and *Terniopsis australis* (C. Cusset & G. Cusset) M. Kato) (Kato *et al.* 2003; Kato 2009). Thailand is inhabited by at least 42 species of 10

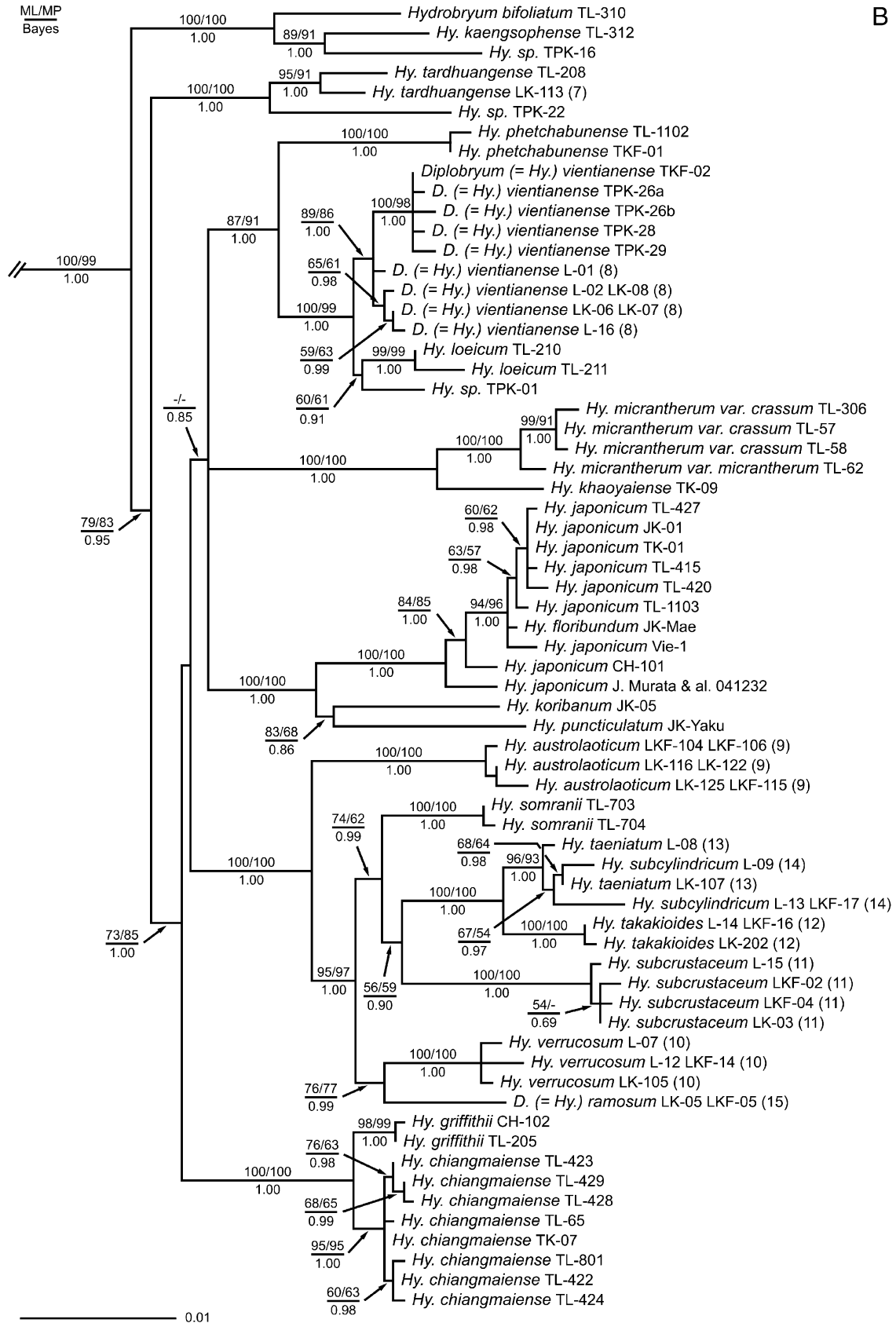


Fig. 1. (continued)

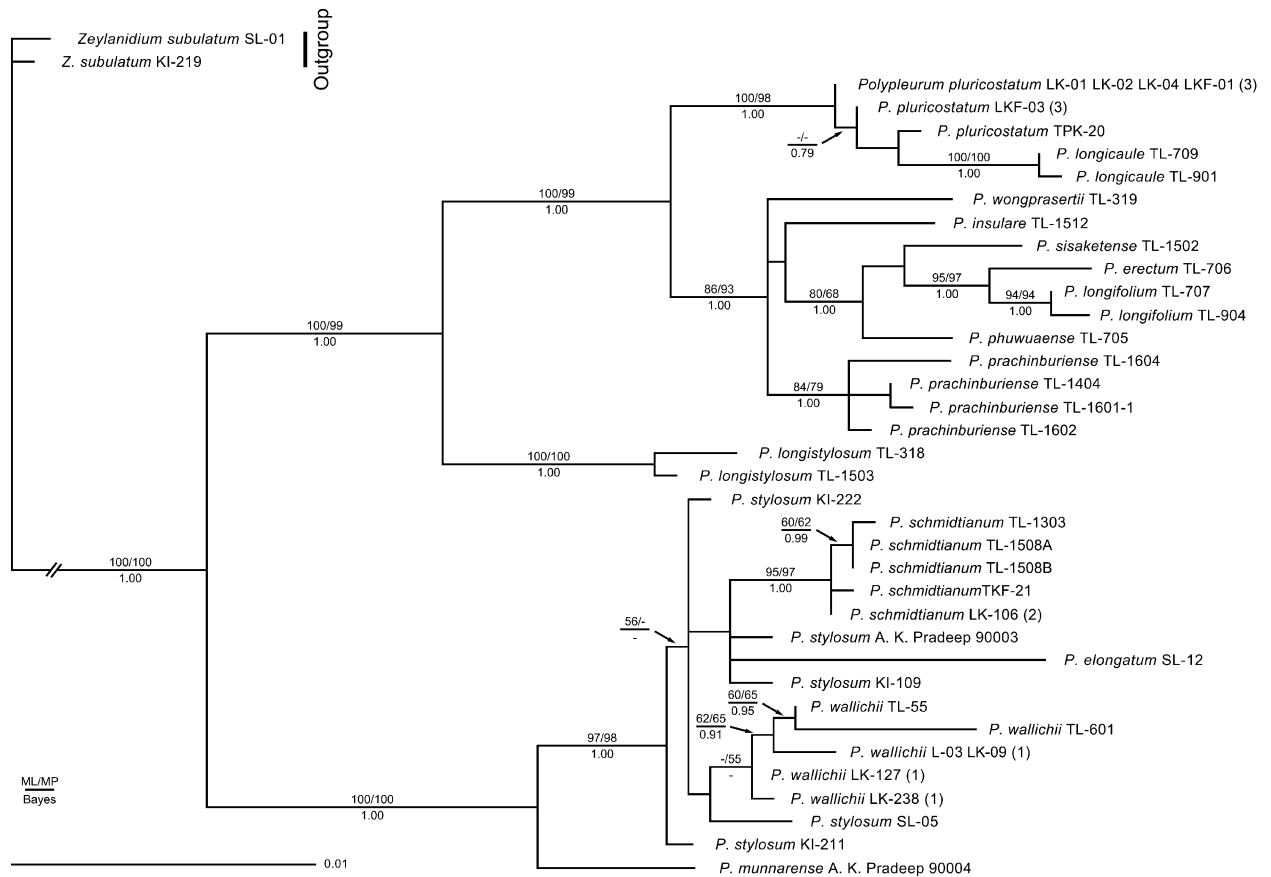


Fig. 2. ML phylogenetic tree of *matK* of *Polypleurum* clade including *Griffithella*. Numbers above and below branches indicate bootstrap supports (>50 %) of ML (left) and MP (right), and posterior probabilities (>0.50) of Bayesian analyses, respectively. *Zeylanidium subulatum* is treated as an outgroup. Numbers in parentheses following species names are species numbers used in this paper.

genera, the largest number in Asia, a few of which belong in small genera endemic to Thailand, i.e., *Hanseniella* and *Thawatchaia* (Kato 2004, 2006a; Kato & Koi 2009).

All Lao genera except *Hydrodiscus* are distributed in Thailand, while most species of Laos are endemic. Thus, Laos and Thailand together shape a centre of distribution for Podostemaceae in SE Asia. This region is considered to be the secondary centre of

diversification for the subfamily Podostemoideae, which likely underwent primary diversification in tropical America (Kita & Kato 2001; Kato 2006b, 2009).

The genus *Hydrobryum*, the largest of the Lao genera, comprises 9 species, which, along with the related genera, are discriminated by their multiple diagnostic characters, as shown in Table 1 and the Key.

Key to the Podostemaceae species of Laos

1. Root absent; shoots to 1 m long, branched, floating; anchoring base disk-like . . . **6. Hydrodiscus koyamae**
Roots present; shoots reduced (to 2 cm long) 2
2. Roots cylindrical to ribbon-like 3
Roots crustose 10
3. Roots floating at least distally 4
Roots creeping on rock along the entire length 5
4. Roots adhered by disk-like base; tufts of leaves (shoots) and flowers borne only at sinuses of root branches **15. Hydrobryum ramosum**
Roots adhered by proximal parts; tufts of leaves and flowers borne on flank of root between successive branches **1. Polypleurum wallichii**

5. Tufts of leaves and flowers borne on flank of root between successive branches 6
 Tufts of leaves and flowers borne only at sinuses of root branches 7
6. Bracts entire; capsules ellipsoidal, c. 8-ribbed **2. *Polypleurum schmidtianum***
 Bracts trilobed; capsules globose or ellipsoidal, 12 – 14-ribbed **4. *Paracladopus Chiangmaiensis***
7. Bracts digitate; capsules globose or ellipsoidal, smooth **5. *Cladopus pierrei***
 Bracts entire; capsules ellipsoidal, ribbed 8
8. Flowering shoots erect; capsules not flattened **3. *Polypleurum pluricostatum***
 Flowering shoots appressed; capsules flattened 9
9. Roots to 1 mm wide; stamen 1 **14. *Hydrobryum subcylindricum***
 Roots 1 – 2 mm wide; stamens 2 **13. *Hydrobryum taeniatum***
10. Flowering shoots erect, 7 – 14 mm long; bracts terete, subulate **12. *Hydrobryum takakioides***
 Flowering shoots appressed, much shorter; bracts flat, ovate 11
11. Stamens 1; ovaries 1-locular **9. *Hydrobryum austrolaoticum***
 Stamens 2; ovaries 1- or 2-locular 12
12. Ovaries 1-locular, subsessile, stalks 0.1 – 0.5 mm long; ovaries matured within spathella
 **11. *Hydrobryum subcrustaceum***
 Ovaries 2-locular, stalks 0.3 – 2 mm long; ovaries at least partly protruded from spathella 13
13. Bracts distally acute to linear; basal part of ovaries enclosed by spathella **7. *Hydrobryum tardhuangense***
 Bracts ovate, obtuse; ovaries exposed 14
14. Roots adhered to rock by thin pads; stamens forked $\frac{1}{2}$ – $\frac{1}{5}$ from top; ovules 8 – 27 per locule
 **8. *Hydrobryum vientianense***
 Roots adhered by prominent warty projections; stamens forked $\frac{1}{4}$ – $\frac{1}{8}$ from top; ovules 17 – 67 per locule . .
 **10. *Hydrobryum verrucosum***

Taxonomic revision and comparative morphology

Polypleurum (*Taylor ex Tul.*) Warm.; Cusset (1992: 36); Kato (2006a: 35). Type species: *Polypleurum wallichii* (R. Br. ex Griff.) Warm.

About 17 species in tropical Asia; three species in Laos.

NOTES. This genus is characterised by the ribbon-like roots with shoots at the sinuses of root branches or along the flanks between successive root branches, the entire bracts, and the ellipsoidal, slightly flattened, 8- or 12 – 14-ribbed capsules dehiscing by unequal or subequal valves (Kato 2006a). Along with *Zeylanidium* and some small genera, it forms a clade in Podostemoideae different from the *Hydrobryum* clade and *Cladopus* clade (Kita & Kato 2001; S. Koi, unpubl. data).

1. *Polypleurum wallichii* (R. Br. ex Griff.) Warm. (Warming 1901b: 57); Cusset (1992: 42, f. 8); Kato (2006a: 36, f. 14). Type: India, Cherrapunji, Griffith s.n. (holotype K!).

Roots floating, attached to rock surface with proximal parts, ribbon-like, 3 – 5 mm wide, c. 1 mm thick, irregularly branched; leaves a few per tuft, linear-oblong, to 5 mm long, on both flanks of root between root branches and at sinuses of root branching. Flowering shoots on both flanks of root between successive root branches and at sinuses

of root branching, solitary, appressed or oblique, flowers oblique to erect; bracts 3 – 4 in 2 files, lanceolate to ovate-lanceolate, sheath-like base, apex acute or acuminate (often caducous), 6 – 9 mm long; spathella enclosing young flower, ellipsoidal, obtuse, c. 3 – 6 mm long, ruptured near apex at anthesis; pedicels 7 – 13 mm long; tepals 2, on each side of stamen, linear, 1 – 1.5 mm long; stamens 2 with andropod, forked $\frac{1}{2}$ – $\frac{1}{4}$ from tip, 2.5 – 3 mm long, as long as pistil; anthers elliptic, 0.7 – 0.9 mm long; ovaries single, sessile, 2-locular, ellipsoidal, 2 – 2.5 mm long, 1 – 1.2 mm wide; stigmas 2, papillate, forked at base, subulate to narrowly triangular, entire, equal or subequal, 0.3 – 0.8 mm long; ovules 56 – 89 per locule, borne on whole placenta surface; capsule-stalks 4 – 16 mm long, capsules ellipsoidal, 2 – 2.5 mm long, 1 – 1.2 mm wide, 8 (– 10)-ribbed, dehiscing by 2 unequal valves. Fig. 3.

DISTRIBUTION. Northern, central and southern Laos; northern and southern India, SE Burma, Thailand, possibly also Cambodia.

SPECIMENS EXAMINED. LAOS. Vientiane prov.: Hinkhanna waterfall, 200 m alt., 18°03'28.0"N, 102°28'29.7"E, fr. Jan., M. Kato et al. L-03; loc. cit., fl. fr. Dec., S. Koi & T. Wongprasert LK-09; Khu Kanna Nam Tok (= Hinkhanna waterfall), N. Fukuoka & T. Koyama L-65097 (TNS). Sekong prov.: Tad Faek waterfall, 123 m alt., 15°14'37.9"N, 106°44'57.3"E, fr. Feb., S. Koi & T. Wongprasert LK-238. Attapeu prov.: Tad Hiew Khon waterfall, Ban Muen Hua Mueang, 137 m alt., 15°13'45.4"N, 106°44'46.8"E, fl. fr. Jan., S. Koi et al. LK-127.



Fig. 3. *Polypleurum wallichii*. A root with flowering shoots on flank; B tuft of leaves; C young flower enclosed by spathe and subtended by bracts; D young flower with 1 ovary, 2 stamens on common andropod and 2 tepals (1 not seen), protruding from ruptured spathe and bracts; E flower with anthers fallen, spathe and bracts; F fruit, side view; G ovules on septum in 2-locular capsule with valve removed. From M. Kato et al. L-03. DRAWN BY M. NAKAJIMA.

HABITAT. Epilithic on seasonally submerged rocks in waterfalls in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a few spots; widely and patchily distributed in Asia.

NOTES. This is the most widely distributed species in the genus, ranging from India to northern Laos. It is closely related to Indian and Sri Lankan *Polypeurum elongatum* (Gardner) J. B. Hall and *P. stylosum*, with which it shares the shoots borne along the flanks of the root and the two stamens. *P. wallichii* is also close to *P. schmidtianum*, but differs in the root partly floating (vs entirely adhering to the rock in *P. schmidtianum*) and the two stamens.

The Lao plant is referable to var. *wallichii*, while var. *parvum* M. Kato is restricted to central Thailand (Kato 2006a).

2. *Polypeurum schmidtianum* Warm. (Warming 1901a: 258; 1901b: 3, f. 1–6); Cusset (1992: 38); Kato (2006a: 40). Type: Thailand, Klong Sarlakpet, Koh Chang, 600 ft, Schmidt s.n. (C 3160).

Polypeurella schmidtiana (Warm.) Engl. (Engler 1927: 9).

Roots ribbon-like, 1.2–2 mm wide, 0.8 mm thick, irregularly and often branched. *Flowering shoots* on both flanks of root between successive branches and at sinuses of root branching, solitary, appressed; bracts 3–4 in 2 files, uniform, lanceolate to ovate, sheath-like base, apex linear (caducous), 1.8–2.5 mm long; spathe enclosing young flower, ellipsoidal, obtuse, 2–2.5 mm long, smooth on dorsal side, minutely papillate on the apical part on ventral side, ruptured near apex at anthesis, persistent; pedicels 3–7 mm long; tepals 2, on each side of stamen, linear, c. 1 mm long; stamen 1, 2–3 mm long, as long as pistil; anthers elliptic, 0.5–0.7 mm long; ovaries single, sessile, 2-locular, ellipsoidal, 1.2–2 mm long, 0.8–1 mm wide; stigmas 2, forked at base, subulate, entire, equal or unequal, 0.5–1 mm long; ovules 25–42 per locule, borne on whole placenta surface; capsule-stalks 3–13 mm long, capsules ellipsoidal, c. 1.8 mm long, c. 0.8 mm wide, 8–9-ribbed, dehiscing by 2 unequal valves. Fig. 4.

DISTRIBUTION. Northern central Laos; SE Thailand.

SPECIMEN EXAMINED. LAOS. Bolikhamsai prov.: Tad Nampa waterfall, Nam Nampa R., Ban Nampa, 163 m alt., 18°30'47.7"N, 103°36'26.8"E, fl. fr. Jan., *S. Koi et al.* LK-106.

HABITAT. Epilithic on seasonally submerged rocks in waterfalls in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a single waterfall.

NOTES. This was recorded from SE Thailand (Trat province including Ko Chang), so the Lao population is isolated from it. The Lao specimen differs from Thai

specimens in the narrower root (vs 2–4 mm wide in Thai specimens), the longer stamen (2–3 mm vs c. 1.2 mm), and the larger ovary (1.2–2 mm vs 1.2–1.6 mm) with the longer stigmas (0.5–1 mm vs 0.2–0.5 mm). Nevertheless, they have identical *matK* sequences.

3. *Polypeurum pluricostatum* Koi & M. Kato sp. nov.

a *P. wallichii* et *P. schmidtiano* foliis ad ramificationibus radices differt, *P. wongprasertii* M. Kato simillissimum, sed stamine ovario longiore, capsulis pluricostatis differt, *P. prachinburiensis* M. Kato & Koi simillissimum, sed stigmatibus longioribus differt. Typus: Laos, Vientiane prov., Nam Mang 3 Dam, Mt Phuu Khao Khouay, 700 m alt., 18°21'26.8"N, 102°48'28.6"E, *S. Koi, R. Fujinami, N. Katayama & T. Wongprasert* LKF-03 (holotypus TNS!; isotypus BKF!).

<http://www.ipni.org/urn:lsid:ipni.org:names:77120300-1>

Roots ribbon-like, 1.5–3.5 mm wide, isotomously or anisotomously branched; leaves to 7 per tuft, needle-like, sheath-like base, to 20 mm long, on dorsal surface of root at sinuses of root branching. *Flowering shoots* on dorsal surface of root at sinuses of root branching, solitary, erect; bracts 2–5 in 2 files, uniform, triangular, apex acute, acuminate, needle-like or linear (caducous), 1–15 mm long, scaly-papillate; spathe enclosing young flower, ellipsoidal, 2–4 mm long, scaly-papillate, ruptured near apex at anthesis, persistent; pedicels 1–6 mm long; tepals 2, on each side of stamen, linear, 1 mm long; stamens 1, 1.5–3 mm long, as long as pistil; anthers elliptic, c. 0.8 mm long; ovaries single, sessile, 2-locular, ellipsoidal, 1.2–2 mm long, 1–1.2 mm wide; stigmas 2, forked at base, linear to subulate, entire, equal or subequal, 0.5–0.8 mm long; ovules 14–64 per locule, borne on whole placenta surface (sometimes except in central area); capsule-stalks 1.5–6.5 mm long, capsules ellipsoidal, 1.2–2 mm long, c. 1 mm wide, 12–14-ribbed, dehiscing by 2 unequal or subequal valves. Fig. 5.

DISTRIBUTION. Northern central Laos; NE Thailand.

SPECIMENS EXAMINED. LAOS. Vientiane prov.: Nam Mang 3 Dam, Mt Phuu Khao Khouay, 700 m alt., 18°21'26.8"N, 102°48'28.6"E, fl. fr. Dec., *S. Koi & T. Wongprasert* LK-01; *loc. cit.*, fl. Dec., *S. Koi & T. Wongprasert* LK-02; *loc. cit.*, fl. fr. Dec., *S. Koi & T. Wongprasert* LK-04; *loc. cit.*, fl. fr. Jan., *S. Koi et al.* LKF-01; *loc. cit.* fl. fr. Jan., *S. Koi et al.* LKF-03 (type).

HABITAT. Epilithic on seasonally submerged rocks in rapids in open place.

CONSERVATION STATUS. Near threatened (NT): collected from a single spot.

NOTES. This is distinct from *Polypeurum wallichii* and *P. schmidtianum*, but apparently very similar to Thai congeners, in the tufts of leaves at the sinuses between

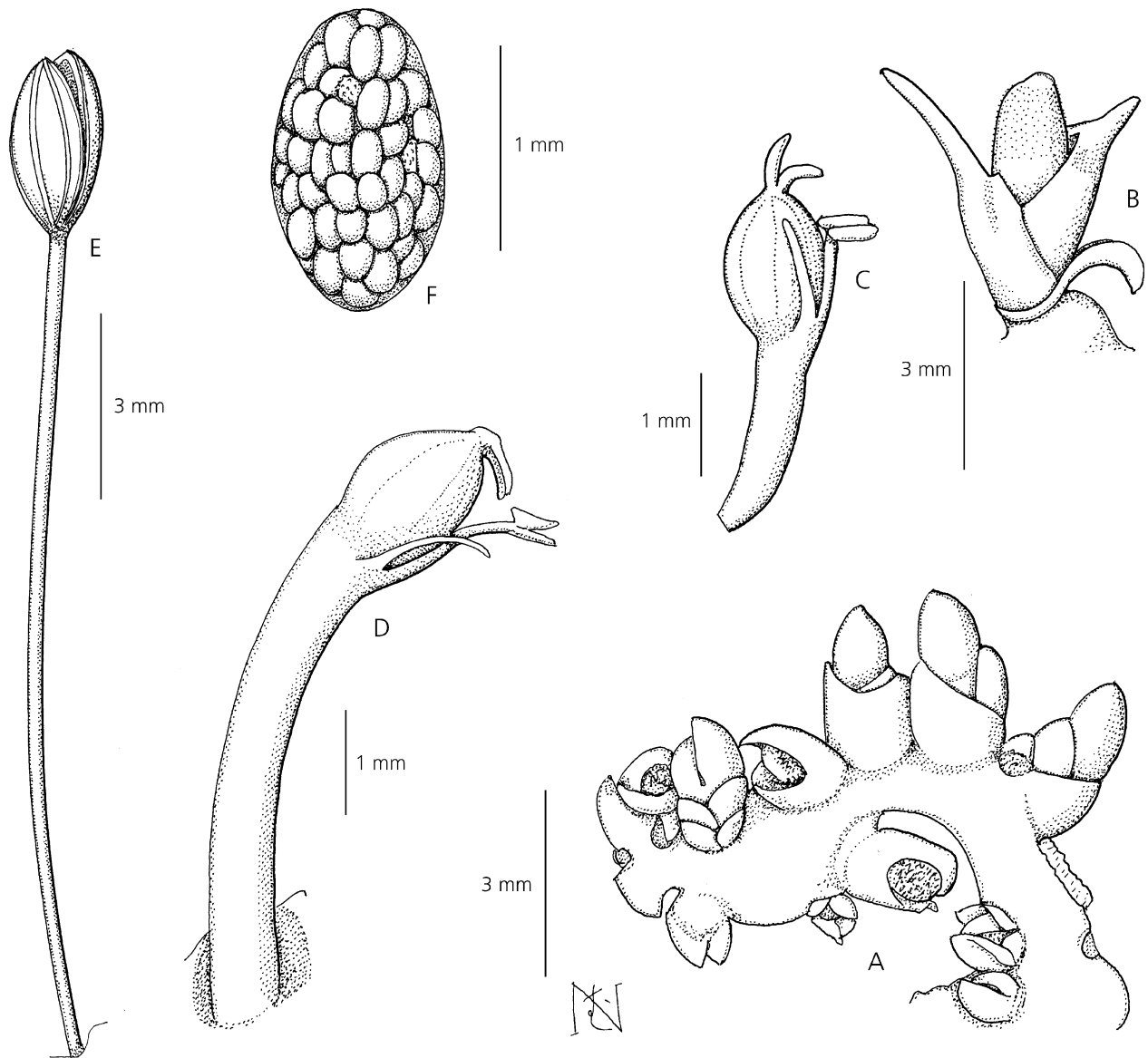


Fig. 4. *Polypeurum schmidtianum*. A ribbon-like root with young flowering shoots on flank; B young flower enclosed by spathe and subtended by bracts; C young flower protruding from ruptured spathe (not drawn); D flower with 1 ovary, 1 stamen and 2 tepals (1 not seen); E fruit with dehiscing capsule on elongate stalk; F ovules on ovary septum. From S. Koi *et al.* LK-106. DRAWN BY M. NAKAJIMA.

root branches, for example: *P. wongprasertii* M. Kato, *P. longifolium* M. Kato, *P. phuwaense* M. Kato, *P. longicaule*, *P. erectum* M. Kato, *P. sisaketense* M. Kato & Koi, *P. prachinburiense* M. Kato & Koi, and *P. insulare* M. Kato & Koi (Kato 2006a; Kato & Koi 2009). *P. pluricostatum* is most similar to *P. wongprasertii* and *P. prachinburiense*, but differs from the former in the length of stamen (1.5 – 3 mm vs 1 – 1.2 mm in *P. wongprasertii*) and the number of capsule ribs (12 – 14 vs 10 – 12), and from the latter in the length of stigma (0.5 – 0.8 mm vs 0.2 – 0.4 mm). The species is also discriminated from *P. longifolium* in the shorter leaves (to 20 mm vs 20 – 40 mm); from *P. phuwaense* in the shorter pedicel (1 – 6 mm vs 10 – 15 mm) and shorter capsule-stalk (1.5 – 6.5 mm vs 8 – 12 mm); from

P. erectum in the wider roots (1.5 – 3.5 mm vs 1 – 1.5 mm), fewer bracts (2 – 5 vs many), shorter capsule-stalk (1.5 – 6.5 mm vs 12 – 20 mm); from *P. sisaketense* in the linear (vs hemicircular) and longer stigmas (0.5 – 0.8 mm vs 0.1 – 0.2 mm); and from *P. insulare* in the greater number of ovules (14 – 64 vs 10 – 12) and greater number of capsule-ribs (12 – 14 vs 8 – 12).

Phylogenetically, *Polypeurum pluricostatum* includes, or is the closest to, *P. longicaule* (Fig. 2). However, morphologically *P. longicaule* is distinct from *P. pluricostatum* in the long (to 18 cm long), branched floating shoots, the broad (2.5 – 5 mm) root and the long (5 – 20 mm) capsule-stalk. In the elongate shoot, which is apomorphic in *Polypeurum*, *P. longicaule* is a derived species, and the paraphyletic *P. pluricostatum* is ancestral.

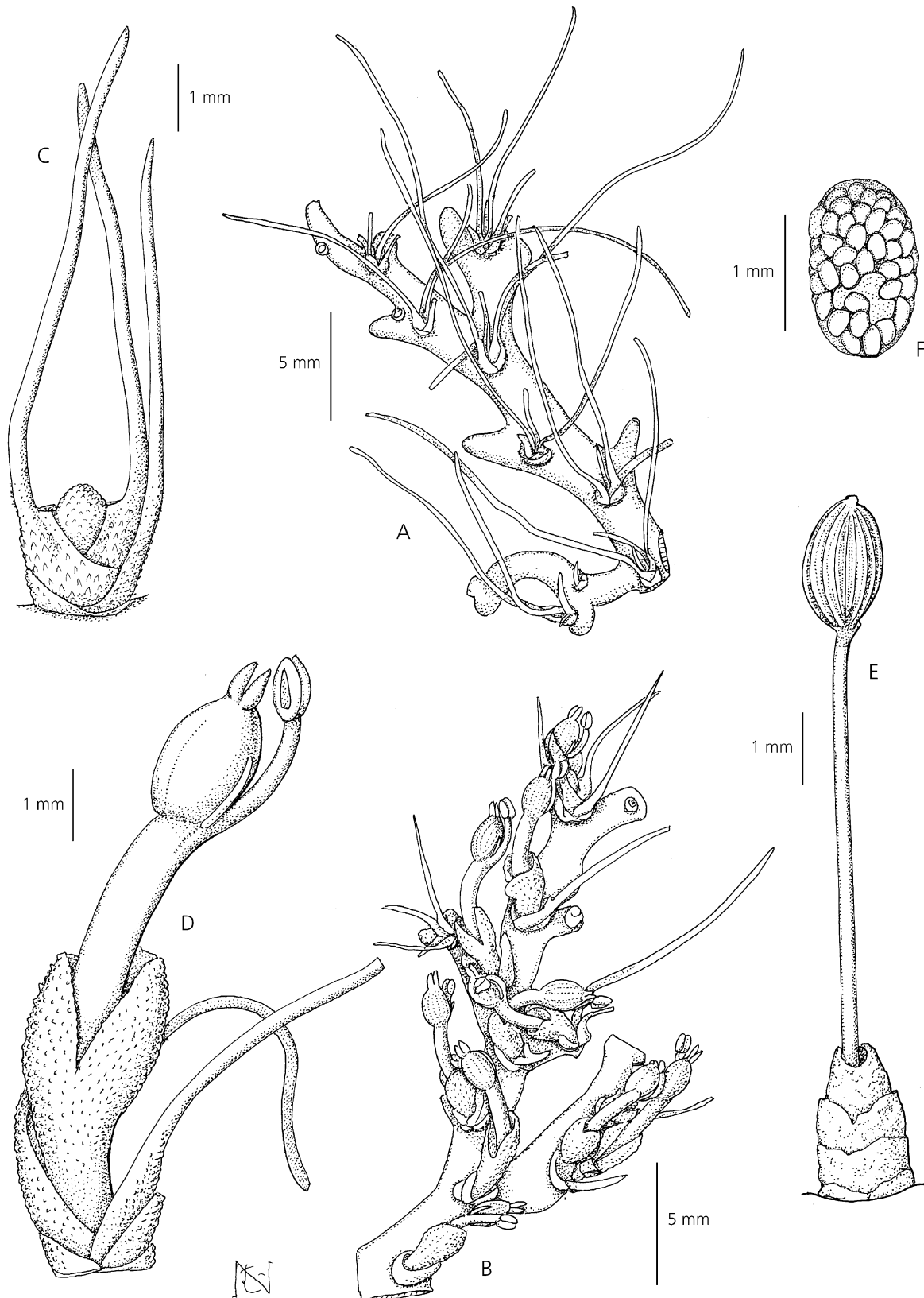


Fig. 5. *Polypleurum pluricostatum*. **A** ribbon-like root with tufts of leaves at sinuses of root branches; **B** root with flowering shoots at sinuses of root branches; **C** young flower enclosed by spathe and subtended by bracts; **D** flower with 1 ovary, 1 stamen and 2 tepals (1 not seen), protruding above ruptured spathe and bracts; **E** fruit with elongate stalk, ruptured spathe and bract remains, side view; **F** ovules on ovary septum with lower central sterile area. From S. Koi *et al.* LKF-03. DRAWN BY M. NAKAJIMA.

Paracladopus *M. Kato (2006a: 29); Koi et al. (2008: 202, emended)*. Type: *Paracladopus chiangmaiensis* M. Kato. Two species in Thailand; one species in Laos.

NOTES. This genus is sister to *Cladopus* (Fig. 1A) and differs from it in the vegetative shoots (tufts of leaves) and flowering shoots borne on the flanks of the root between successive branches and the ribbed capsules. *Paracladopus chiangmaiensis* and *P. chanthaburiensis* are distinct from each other morphologically and molecular-phylogenetically (Koi et al. 2008; Fig. 1A). *P. chiangmaiensis* occurs in several spots in southern Laos and in a few spots in Chiang Mai province, northern Thailand, while *P. chanthaburiensis* is known in a narrow area in Chanthaburi province, south-eastern Thailand.

4. *Paracladopus chiangmaiensis* *M. Kato (2006a: 29, f. 11)*. Type: Northern Thailand, Chiang Mai prov., Mae Wang stream, N of Doi Inthanon National Park, 450 m alt., 18°38'N, 98°43'E, fl. fr. March, *M. Kato, R. Imaichi & T. Wongprasert* TL-808 (holotype BKF!; isotype TNS!).

Roots ribbon-like, 0.8 – 2.5 mm wide, isotomously or anisotomously branched, adhering to rock surface with rhizoid pads distributed in centre of root and by holdfasts at shoot bases on ventral side; holdfasts cylindrical, to 0.6 mm long; leaves to 6 per tuft, ensiform with lamina flat in adaxial-abaxial plane, linear-oblong, sheath-like base, apex obtuse, to 4.5 mm long, on both flanks of root between successive root branches and at sinuses of root branching. *Flowering shoots* on both flanks of root between root branches and at sinuses of root branching, solitary, appressed; bracts 3 – 11, uniform, trilobed, 0.8 – 1.8 mm long; spathe enclosing young flower, ellipsoidal, mucronate, 1 – 2 mm long, ruptured near apex at anthesis; pedicels 0.5 – 1.5 mm long; tepals 2, on each side of stamen, linear, 0.3 – 0.8 mm long; stamen 1, 1.2 – 1.6 mm long, as long as pistil; anthers elliptic c. 0.2 mm long, caducous; ovaries single, sessile, 2-locular, globose or ellipsoidal, 0.8 – 1.4 mm long, 0.6 – 1 mm wide; stigmas 2, forked at base, narrowly triangular, entire, equal, 0.3 – 0.5 mm long; ovules 16 – 45 per locule, borne on whole placenta surface; capsule-stalks 0.6 – 1.8 mm long, capsules globose or ellipsoidal, 0.8 – 1.4 mm long, 0.6 – 1 mm wide, 12 – 14-ribbed, dehiscent by 2 unequal or subequal valves. Fig. 6.

DISTRIBUTION. Southern Laos; northern Thailand.

SPECIMENS EXAMINED. **LAOS.** Salavan prov.: Tad Lo waterfall, 350 m alt., 15°31'36.1"N, 106°16'22.3"E, st. Jan., *S. Koi et al.* LKF-116; Huay Taphung R., at the point crossing Route 20, 500 m alt., 15°27'59.7"N, 106°10'12.3"E, st. fl. fr. Jan., *S. Koi et al.* LKF-119.

Champasak prov.: Tad Pha Suam waterfall, Bajiang National Park, 200 m alt., 15°16'33.3"N, 105°55'19.2"E, fl. fr. Feb., *S. Koi & T. Wongprasert* LK-213; *loc. cit.*, st. fl. fr. Jan., *S. Koi et al.* LKF-110; Houay Pa Lai R., Ban Kaeng Yao, Bajiang, 227 m alt., 15°20'7.0"N, 105°58'55.2"E, st. Feb., *S. Koi & T. Wongprasert* LK-220; Huay Ka Pheu R., at the point crossing Route 20, 450 m alt., 15°24'33.6"N, 106°05'28.5"E, st. fl. Feb., *S. Koi & T. Wongprasert* LK-223; *loc. cit.*, st. fl. fr. Jan., *S. Koi et al.* LKF-121; Houay Champy R., at the point crossing Route 20, 200 m alt., 15°15'30.6"N, 105°55'59.5"E, fl. fr. Jan., *S. Koi et al.* LKF-105.

HABITAT. Epilithic on seasonally submerged rocks in waterfalls and rapids in open places.

CONSERVATION STATUS. Near threatened (NT): collected from several spots.

NOTES. This is the first record of the genus from Laos. The clade of *Paracladopus chiangmaiensis* is divided into two subclades: one consists of Thai and Lao plants and the other consists of only Lao plants (Fig. 1A). The plants of the former clade have more bracts than those of the latter. South-eastern Thai *P. chanthaburiensis* is geographically close to, but distinct from, *P. chiangmaiensis* in the digitate bracts and two stamens (Koi et al. 2008).

Cladopus *H. A. Möller (1899: 115); Cusset (1992: 20) excl. Griffithella (Tul.) Warm.; Kato & Kita (2003: 90); Kato (2006a: 3)*. Type: *Cladopus nymani* H. A. Möller. *Lecomtea* Koidz. (Koidzumi 1929: 52). Type: *Lecomtea pierrei* (Lecomte) Koidz. *Torrenticola* Steenis (1949: 66). Type: *Torrenticola queenslandica* (Domin) Domin ex Steenis.

About nine species in E and SE Asia; one species in Laos.

NOTES. *Torrenticola* had been segregated as a monotypic genus characterised by the elongate shoots with trifid leaves (bracts) and weakly ribbed capsules (van Steenis 1949; Aston 1990). Kita & Kato (2001) showed that phylogenetically it is nested within *Cladopus*, and Cook & Rutishauser (2001) combined them. Mathew & Sathesh (1997) separated the genera *Cladopus* and *Griffithella* (Tul.) Warm. by the root habit, but Cusset (1992) treated them as sections of the genus *Cladopus* based on the shared smooth-surfaced capsule and the number of stamens (1 vs 2). Section *Griffithella* (Tul.) C. Cusset is excluded from the genus (see also notes below).

5. *Cladopus pierrei* (*Lecomte*) *C. Cusset (1973a: 73, pl. 10, f. 7 – 9; 1992: 25)*. Type: Laos, Champasak, Bassac, *F.(A.) F. J. Harmand* s.n. (as *Pierre* 5194) (P!).

Roots ribbon-like, 1 – 4 (– 7) mm wide, isotomously or anisotomously branched; leaves to 10 per tuft, linear, to 3.5 mm long, on dorsal surface of root at sinuses of

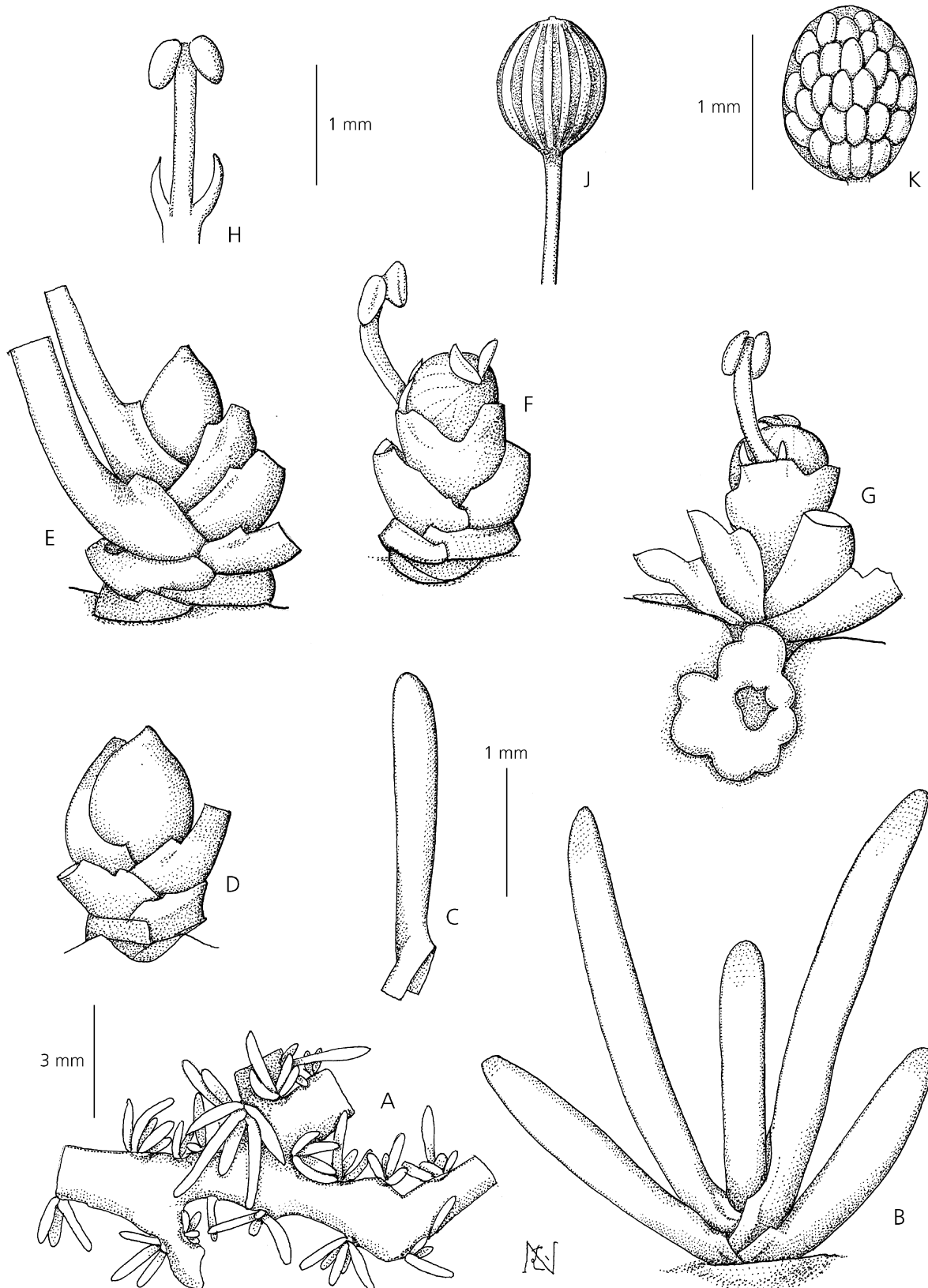


Fig. 6. *Paracladopus chiangmaiensis*. A ribbon-like root with tufts of leaves on flank; B 2-fariate ensiform leaves; C leaf; D, E young flowers enclosed by spathe and subtended by bracts (distal part of bract is fallen); F flower with 1 ovary, 1 stamen and 2 tepals, partly protruding from ruptured spathe subtended by bracts, dorsal view; G flower with ruptured spathe and bracts on flank of root with holdfast on ventral side, ventral view; H stamen and 2 tepals; J fruit; K ovules on ovary septum. From S. Koi *et al.* LKF-110. DRAWN BY M. NAKAJIMA.

root branching. *Flowering shoots* on dorsal surface of root at sinuses of root branching, solitary, erect; bracts 8 – 10 in 2 files, digitate with 5 – 10 lobes, lobes cylindrical, hard, membranous base, 1 – 2 mm long, papillate with silica; spathella enclosing young flower (which is inclined inside spathella), ellipsoidal, flattened, mucronate, 1.3 – 3.2 mm long, ruptured irregularly at apex at anthesis; pedicels 1 – 5 mm long; tepals 2, on each side of stamen, linear, 0.6 – 1.2 mm long; stamens 1, or 2 with andropod, forked above middle or near base, 1 – 3 mm long, as long as, or shorter than, pistil; anthers elliptic, 0.3 – 0.8 mm long, caducous; ovaries single, sessile, 2-locular, globose or ellipsoidal, 0.9 – 2 mm long, 0.6 – 1.6 mm wide; stigmas 2, forked at base, linear to narrowly oblong, equal, 0.5 – 1 mm long; ovules 14 – 78 per locule, borne on whole placenta surface; capsule-stalks 1 – 5 mm long, capsules chestnut-brown, globose or ellipsoidal, 0.9 – 2 mm long, 0.7 – 1.5 mm wide, smooth but with two stripes, dehiscing by 2 unequal or subequal valves. Fig. 7.

DISTRIBUTION. Central and southern Laos; southern Vietnam.

SPECIMENS EXAMINED. LAOS. Khammouan prov.: Nakai-Nan Theun Biological Conservation Area, Jan. 1978, *T. C. Whitmore* s.n. (E) (which comprises fragmentary flowers and fruits, so more complete material is needed for identification). Savannakhet prov.: Sammataek rapid, Muang Phin, 150 m alt., 16°18'03.4"N, 105°58'56.8"E, fr. Feb., *S. Koi & T. Wongprasert* LK-211. Salavan prov.: Kaeng Koo rapid, Vapy Distr., 141 m alt., 15°42'31.7"N, 106°04'08.1"E, fl. fr. Feb., *S. Koi & T. Wongprasert* LK-232; Huay Taphung R., at the point crossing Route 20, 500 m alt., 15°27'59.7"N, 106°10'12.3"E, fl. fr. Jan., *S. Koi et al.* LKF-118. Champasak prov.: Bassac, *F.(A.) F. J. Harmand* s.n. (as *Pierre* 5194) (type, P); Tham Champee waterfall, 936 m alt., 15°12'12.5"N, 106°07'59.2"E, st. fl. fr. Jan., *S. Koi et al.* LK-117; Tat Yuang waterfall, 957 m alt., 15°10'50.4"N, 106°08'18.8"E, st. fl. fr. Jan., *S. Koi et al.* LK-121; *loc. cit.*, st. Jan., *S. Koi et al.* LK-123; Tad Champy waterfall, 137 m alt., 15°17'41.0"N, 105°51'36.6"E, fl. fr. Feb., *S. Koi & T. Wongprasert* LK-214; Houay Pa Lai R., Ban Kaeng Yao, Bajiang, 227 m alt., 15°20'7.0"N, 105°58'55.2"E, fl. fr. Feb., *S. Koi & T. Wongprasert* LK-221; Huay Ka Pheu R., at the point crossing Route 20, 450 m alt., 15°24'33.6"N, 106°05'28.5"E, st. fl. fr. Feb., *S. Koi & T. Wongprasert* LK-222; *loc. cit.*, fl. fr. Jan., *S. Koi et al.* LKF-120; Houay Champy R., at the point crossing Route 20, 200 m alt., 15°15'30.6"N, 105°55'59.5"E, fl. fr. Jan., *S. Koi et al.* LKF-103; Tad Pha Suam waterfall, Bajiang National Park, 200 m alt., 15°16'33.3"N, 105°55'19.2"E, st. fl. fr. Jan., *S. Koi et al.* LKF-109. Sekong prov.: Tad Faek waterfall, 123 m alt., 15°14'37.9"N, 106°44'57.3"E, fr. Feb., *S. Koi & T. Wongprasert* LK-237. Attapeu prov.: Tad Hiew Khon

waterfall, Ban Muen Hua Mueang, 137 m alt., 15°13'45.4"N, 106°44'46.8"E, fl. fr. Jan., *S. Koi et al.* LK-128; Tad Nam Pa (Tad Jo) waterfall, Ban Xan Sai, 129 m alt., 14°56' N, 107°03'01.7"E, fl. fr. Jan., *S. Koi et al.* LK-132; Sekong R., Kaeng Mueang, Lavy village, 106 m alt., 15°18'03.3"N, 106°42'43.3"E, st. fl. fr. Jan., *S. Koi et al.* LK-134; *loc. cit.*, fl. fr. Feb., *S. Koi & T. Wongprasert* LK-241.

HABITAT. Epilithic on seasonally submerged rocks in waterfalls and rapids in open places.

CONSERVATION STATUS. Near threatened (NT): collected from several spots in a broad area.

NOTES. This species is variable in the root width and the number of stamens. The phylogenetic result shows that the clade of this species includes *Cladopus doianus* (= *C. japonicus* Imamura) and is divided into three subclades, one of which is a subclade comprising two forms, i.e., *C. doianus* with single or occasionally two or more stamens and *C. pierrei* p.p. (= LK-128, 132, 134, 232, 237, 241) with two stamens; the second is *C. pierrei* p.p. (= LK-211) with broad root (5 – 7 mm wide) and two stamens; and the third is the remaining *C. pierrei* p.p. (= LK-117, 121, 123, 214, 221, 222; LKF-103, 109, 118, 120) with dominantly single stamens (Fig. 1A). This division is in contrast to the geography that Lao *C. pierrei* is remarkably separated from Japanese and south-eastern Chinese (Fujian) *C. doianus* (= *C. chinensis* H. C. Chao). *C. doianus* differs from *C. pierrei* in the short capsule stalk and the narrow fan-like stigma and possibly in the cleistogamy. *C. pierrei* is likely a paraphyletic ancestral species.

The present analysis indicates a dual phylogenetic feature of *Cladopus* in SE Asia. Lao *C. pierrei*, along with *C. doianus*, belongs to the Northern clade distributed in China and Japan (Kita & Kato 2004), while Thai *C. taiensis* and Thai and Vietnamese *C. fallax* belong to the Southern clade extending to Indonesia, Papua New Guinea and Queensland (Australia).

Cusset (1973a, 1992) divided the genus *Cladopus* into two sections by the number of stamens, *Cladopus* with one stamen and *Griffithella* with two stamens on the common andropod. *C. pierrei* was assigned to the latter as the only SE Asian species. However, the variability of stamens and the phylogeny of *C. pierrei* revealed in this study do not allow separation even at the section level. There are similar variations in the number of stamens in *Hydrobryum* and *Polypleurum* (Kato 2004, 2006a). *Koi et al.*'s (2012) molecular phylogenetic analysis suggests that southern Indian *C. hookerianus* (Tul.) C. Cusset, type of sect. *Griffithella*, belongs to the *Polypleurum-Zeylanidium* clade. Therefore, *C. hookerianus* should be placed in an appropriate genus.

The genus *Lecomtea* Koidz. was proposed for *Cladopus pierrei* (Koidzumi 1929): it is not warranted.

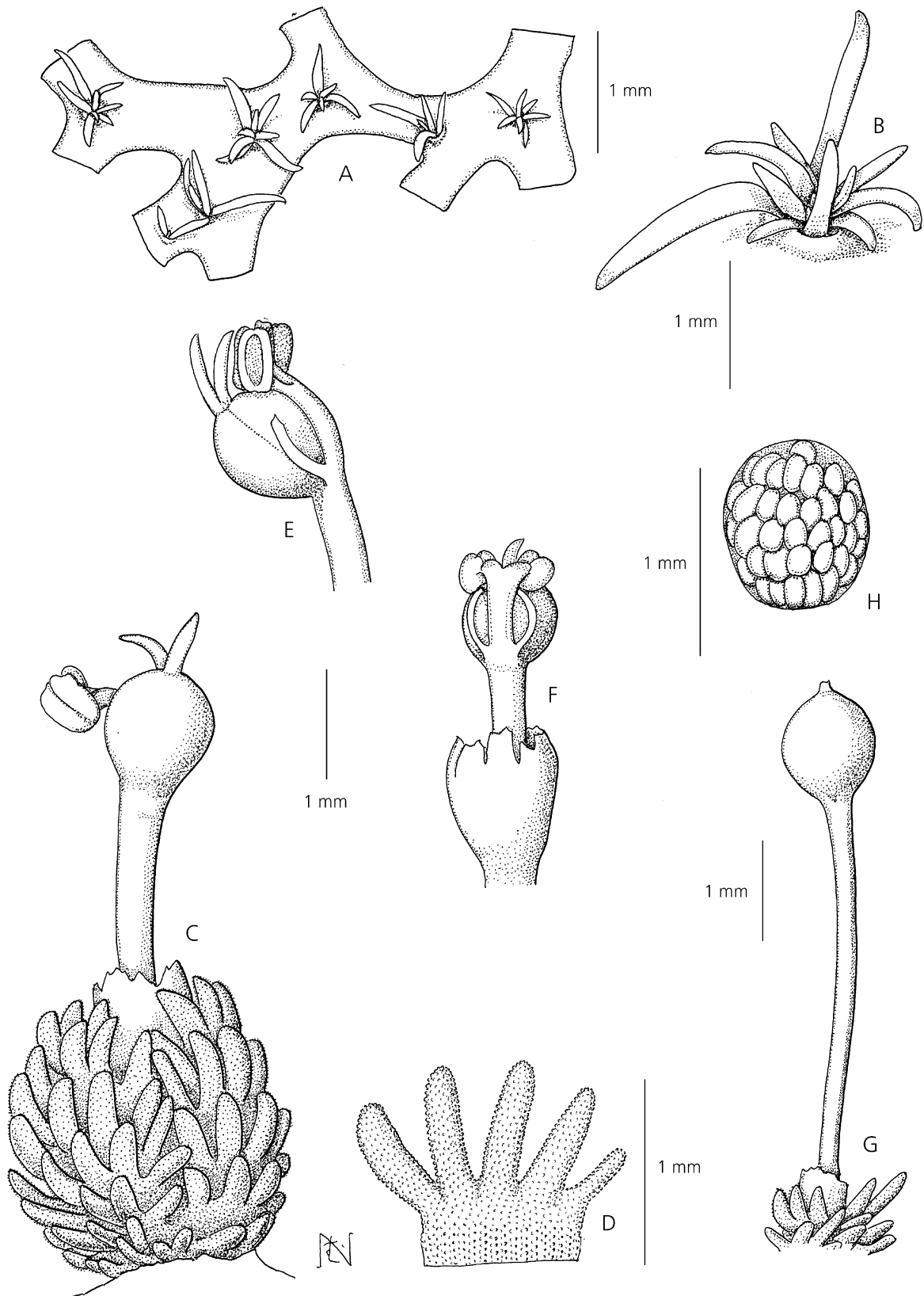


Fig. 7. *Cladopus pierrei*. A ribbon-like root with tufts of leaves at sinuses of root branches; B tuft of leaves; C single-stamened flower protruding from spathe subtended by bracts; D bract; E, F flowers with 1 ovary, 2 stamens on common andropod and 2 tepals: E side view; F ventral view; G fruit with ruptured spathe and bracts at base of stalk; H ovules on ovary septum. From *S. Koi et al.* LKF-109. DRAWN BY M. NAKAJIMA.

Hydrodiscus *Koi & M. Kato* (2010: 387). Type species: *Hydrodiscus koyamae* (M. Kato & Fukuoka) Koi & M. Kato.

DISTRIBUTION. A monotypic genus endemic to Laos.

NOTES. This monotypic genus is phylogenetically sister to the *Hydrobryum* clade including *Hanseniella* and *Thawatchaia* (Koi & Kato 2010; Fig. 1A). *Hydrodiscus* is rootless and has shoots with anchoring disk-like bases and in this character it is unique in Asian Podostemoideae (Koi & Kato 2010). Disk-bearing plants are also seen in some species of African Podostemoideae, which are phylogenetically separated from the Asian Podostemoideae (Kita & Kato 2001; Moline *et al.* 2007). In the absence of roots it is also similar to South American genera, e.g. *Mourea* Aubl. and *Rhyncholacis* Tul., in another clade remote from the Asian clade (Warming 1899; Rutishauser & Grubert 1994; Kita & Kato 2001; S. Koi *et al.* unpubl. data). Since *Hydrodiscus* is placed in the Asian–Australian Podostemoideae, it is likely that the loss of the root happened independently of the African and American clades, and also of *Dalzellia*, subfamily Tristichoideae (Kita & Kato 2001, 2005; Imaichi *et al.* 2004).

6. *Hydrodiscus koyamae* (M. Kato & Fukuoka) Koi & M. Kato (2010: 387, f. 35). Type: Laos, Boli Kham Xai (= Bolikhamsai) prov., Tat Luek Nam Tok (= Tad Leuk waterfall), N. Fukuoka & H. Koyama L-65169 (holotype TNS!; isotypes L!, MO, SHO). *Diplobryum koyamae* M. Kato & Fukuoka (2002: 116, f. 4).

Shoots attached to rock surface with disk-like base, cylindrical, to 1 m long, 0.6 – 1.5 mm in diam., branched many times, glabrous or sparsely scaly-leafy; shorter shoots borne on disk; leaves narrowly-deltoid to deltoid, 1.2 – 1.5 mm long, c. 1 mm wide. Flowering shoots alternate on lateral sides of elongated shoot, solitary or sometimes with 1 or 2 additional lateral flowers, also borne on basal disk; bracts 4 – 7 in 2 files, uniform but basal ones smaller, ovate, sheath-like base, apex acute or acuminate, 3 – 6 mm long; spathella enclosing young flower, narrowly ellipsoidal (fusiform), c. 5 mm long, ruptured near apex at anthesis, persistent; pedicels c. 1 mm long; tepals 2, on each side of stamen, linear, c. 4 mm long; stamens 2 with andropod, forked $\frac{1}{2}$ – $\frac{1}{3}$ from tip, 6 – 10 (– 13) mm long, longer than pistil; anthers oblong, 1.5 – 2 mm long; ovaries single, stalked (stalks 2 – 3 mm long), 2-locular, ellipsoidal, flattened, 3 – 3.5 mm long, 1.2 – 1.5 mm wide, 1 – 1.2 mm thick; stigmas 2, forked above base, linear to narrowly triangular, unequal, 1 – 1.5 mm long; ovules 20 – 41 per locule, borne on whole placenta surface except in small central lower area; capsule-stalks 2 – 4 mm long, capsules ellipsoidal,

slightly flattened, 3 – 3.5 mm long, c. 1.2 mm wide, c. 1 mm thick, 18 – 20-ribbed, dehiscing by 2 equal or subequal valves. Fig. 8.

DISTRIBUTION. Endemic to northern central Laos.

SPECIMENS EXAMINED. LAOS. Bolikhamsai prov.: Tad Leuk waterfall, Phuu Khao Khouay National Park, 200 m alt., 18°23'42.9"N, 103°04'17.0"E, st. fl. fr. Jan., M. Kato *et al.* L-06; *loc. cit.*, N. Fukuoka & H. Koyama L-65169 (type, TNS); Tad Xai waterfall, Phuu Khao Khouay National Park, 300 m alt., 18°27'7.0"N, 103°08'39.5"E, st. fl. fr. Jan., M. Kato *et al.* L-11; *loc. cit.*, 300 m alt., 18°27'18.8"N, 103°08'31.8"E, fl. fr. Jan., S. Koi *et al.* LKF-13; Tad Nampa waterfall, Nam Nampa R., Ban Nampa, 163 m alt., 18°30'47.7"N, 103°36'26.8"E, fl. fr. Jan., S. Koi *et al.* LK-104.

HABITAT. Epilithic on seasonally submerged rocks in waterfalls in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a few spots in a small area.

NOTES. This is known from a very narrow area in northern central Laos. It was originally assigned with doubt to the genus *Diplobryum*, because of superficial analogy of the branched axis to *D. ramosum* (Kato & Fukuoka 2002), which is assignable to *Hydrobryum* (see below). However, the two are remarkably distinct in the body plan (Koi & Kato 2010).

Hydrobryum Endl., emend.; Cusset (1992: 44); Kato (2004: 143). Type: *Hydrobryum griffithii* (Wall. ex Griff.) Tul.

Synstylis C. Cusset (1992: 26). Type species: *Synstylis micranthera* (P. Royen) C. Cusset.

Diplobryum C. Cusset (1972: 279, f. 1; 1973a: 68, f. 11), *p.p.* excl. *D. koyamae*, **synon. nov.** Type species: *Diplobryum minutale* C. Cusset.

Roots crustose, ribbon-like or subcylindrical; shoots reduced as tufts of leaves, scattered on dorsal surface of root or borne at sinuses of root lobing or branching; leaves linear; flowering shoots appressed, or exceptionally elongate and erect; bracts imbricate, ovate, or exceptionally separated, subulate; spathella enclosing young flower, ruptured irregularly near apex or longitudinally at anthesis, persistent; tepals 2 on each side of stamen, linear; stamens 1, or 2 with andropod, as long as, or longer than, pistil; ovaries single, ellipsoidal, mostly flattened, 1- or 2-locular; stigmas 2, forked at or above base, equal or unequal; capsules ellipsoidal, flattened, 12 – 20-ribbed, dehiscing by 2 equal or unequal valves.

DISTRIBUTION. Seventeen species in E and SE Asia and Himalayas; seven endemic species in Laos. Because the species are variable ranging beyond the conventional definition of the genus, it is amended below.

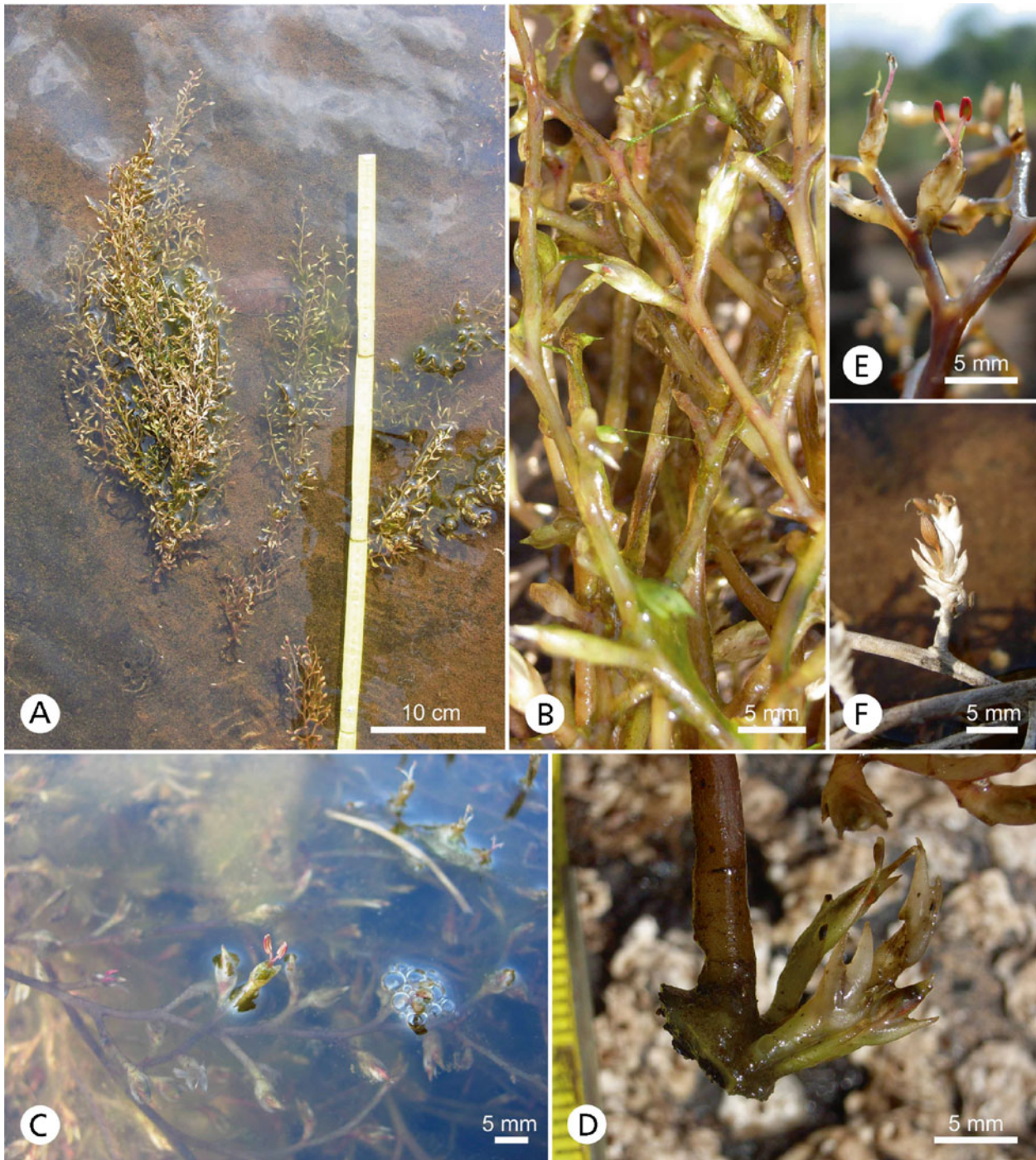


Fig. 8. *Hydrodiscus* (syn. *Diplobryum*) *koyamae*. **A** floating, branched shoots; **B** part of shoot branches with flower buds; **C** flowers emerging from submerged shoot branches; **D** floriferous disk-like base; **E** flowers on shoot branchlets with red-purple anthers; **F** fruit and bracts on dried branchlet. From M. Kato et al. L-06.

NOTES. *Diplobryum* is reduced to *Hydrobryum*, based primarily on the molecular evidence that *D. vientianense*, morphologically close to *D. minutale* (type of *Diplobryum*), is nested within *Hydrobryum* (Koi & Kato 2010; Fig. 1B). Both species and *D. ramosum* are combined with *Hydrobryum* below.

It is difficult to define the morphologically diverse genus *Hydrobryum* by one or a few particular characters, but it is definable by a combination of characters (root, leaf, flowering shoot, bract, stamen, ovary/capsule). This contrasts with the previous simpler definition by the crustose roots, as well as the ovate

entire bracts on reduced flowering shoots, flattened ribbed capsules, and equal capsule-valves (Cusset 1972, 1992; Kato 2004). In the above-described characters, *Hydrobryum* differs from *Cladopus* with digitate bracts and smooth capsules, *Polypleurum* with erect flowering shoots, and *Zeylanidium* with 8-ribbed capsules and prominently unequal capsule-valves (one of which is persistent and the other is caducous). *Hydrobryum* is the most closely related to *Hanseniella* and *Thawatchaia* phylogenetically and morphologically, but distinct in that the bract is entire in *Hydrobryum* while it is bi- and trilobed in *Hanseniella* and *Thawatchaia*, respectively (Kato 2004).

The monophyletic group consisting of Lao species and Thai *Hydrobryum somranii* M. Kato exhibits a remarkable variation of roots: they range from crustose to ribbon-like and subcylindrical. In the ribbon-like and subcylindrical roots, every shoot is borne at a sinus of root branches. This association also occurs in different genera, e.g., *Cladopus*, a part of *Polypleurum* and *Zeylanidium* (Mathew & Satheesh 1997; Hiyama *et al.* 2002; Koi & Kato 2003; Kato 2006a). There is no such association in the crustose roots. The diversification of the roots will be elucidated by analysis of the root apical meristem responsible for the morphology.

7. *Hydrobryum tardhuangense* M. Kato (2004: 148, f. 7). Type: Thailand, Loei prov., Tard Huang International Waterfall, Na Haew National Park, 570 m alt., 17°34'N, 100°59'E, M. Kato, Y. Kita & T. Wongprasert TL-314 (holotype BKF!; isotype TI!).

Roots crustose, irregularly lobed; leaves to 8 per tuft, linear, sheath-like base, to 3 mm long, papillate, scattered on dorsal surface of root, surrounded by raised rings of root tissue. *Flowering shoots* scattered on dorsal surface of root, solitary, erect or oblique; bracts 2 – 3, uniform, ovate or deltoid, entire, apex acute to linear (caducous), 1 – 3.5 mm long, smooth; spathella enclosing young flower, ellipsoidal, 1.5 – 2.2 mm long, minutely papillate in distal part, smooth in basal part, split longitudinally at anthesis, persistent; pedicels c. 0.2 mm long; tepals 2, on each side of stamen, linear, 1 – 2.5 mm long; stamen 2 with andropod, forked $\frac{1}{3}$ – $\frac{1}{4}$ from tip, 3 – 3.5 mm long, as long as, or longer than, pistil; anthers elliptic, c. 0.4 mm long; ovaries single, stalked (stalks c. 0.3 – 1 mm long), 2-locular, ellipsoidal, flattened, 1.5 – 2 mm long, 0.7 – 1 mm wide, 0.6 – 0.8 mm thick; stigmas 2, forked at base, linear to subulate, one apex pointed and the other obtuse, entire, equal, 0.3 – 0.8 mm long, papillate; ovules 13 – 25 per locule, borne on marginal surface of placenta and in small central upper area; capsule-stalks 1 – 1.2 mm long, capsules ellipsoidal, flattened, 1.5 – 2 mm long, 0.7 – 1 mm wide, 0.5 – 0.7 mm thick, 15 – 16-ribbed, dehiscent by 2 equal valves. Fig. 9.

DISTRIBUTION. Northern central Laos; north-eastern Thailand.

SPECIMEN EXAMINED. LAOS. Khammouan prov.: Tad Namsanam waterfall, Ban Khounkham, Ban Namsanam Dist., 260 m alt., 18°13'11.2"N, 104°30'21.6"E, st. fl. fr. Jan., S. Koi *et al.* LK-113.

HABITAT. Epilithic on seasonally submerged rocks in waterfalls in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a single waterfall.

NOTES. This is the first record from Laos: the species is now known from two separate places. The Lao specimen differs from the Thai specimens in having more capsule-ribs (vs 12 – 14 in Thai plants).

8. *Hydrobryum vientianense* (M. Kato & Fukuoka) Koi & M. Kato **comb. nov.** Type: Laos, Vientiane prov., Khu Kanna Nam Tok (= Hinkhanna waterfall), N. Fukuoka & H. Koyama L-65098 (holotype TNS!; isotype L!).

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Diplobryum vientianense M. Kato & Fukuoka, *Acta Phytotax. Geobot.* 53: 115, f. 1, 2 (2002).

Roots crustose, irregularly lobed, adhering to rock surface with rhizoids in pads on ventral side; leaves linear, tufts scattered on dorsal surface of root. *Flowering shoots* scattered on dorsal surface of root, appressed, flower erect or oblique; bracts 3 – 6 in 2 files, uniform but basal ones smaller, ovate, hood-shaped, entire, apex obtuse, 0.8 – 2 mm long, papillate; spathella enclosing young flower, ellipsoidal, flattened, 2 – 2.5 mm long, papillate except in centre, ruptured longitudinally or irregularly on dorsal surface near apex at anthesis, persistent; pedicels 0.5 – 1 mm long; tepals 2, on each side of stamen, linear, 2 – 4 mm long; stamens 2 with flattened andropod, forked $\frac{1}{2}$ – $\frac{1}{5}$ from tip, 2 – 6 mm long, longer than pistil, filaments pale or pink when fresh; anthers elliptic, c. 0.5 mm long; ovaries single, stalked (stalks 1 – 1.5 mm long), 2-locular, ellipsoidal, flattened, 1.8 – 2.5 mm long, 0.8 – 1.1 mm wide, 0.5 – 1 mm thick, light-green when fresh, protruding from spathella; stigmas 2, forked above base, linear, entire, equal or subequal, 0.5 – 2.5 mm long; ovules 8 – 27 per locule, borne on whole placenta surface except in small central lower area; capsule-stalks 1 – 2.5 mm long, capsules ellipsoidal, flattened, 1.7 – 2.5 mm long, 1 – 1.2 mm wide, 0.5 – 0.9 mm thick, 12 – 18-ribbed, dehiscent by 2 equal or subequal valves; seeds ellipsoidal, smooth. Fig. 10.

DISTRIBUTION. Northern central Laos; north-eastern Thailand.

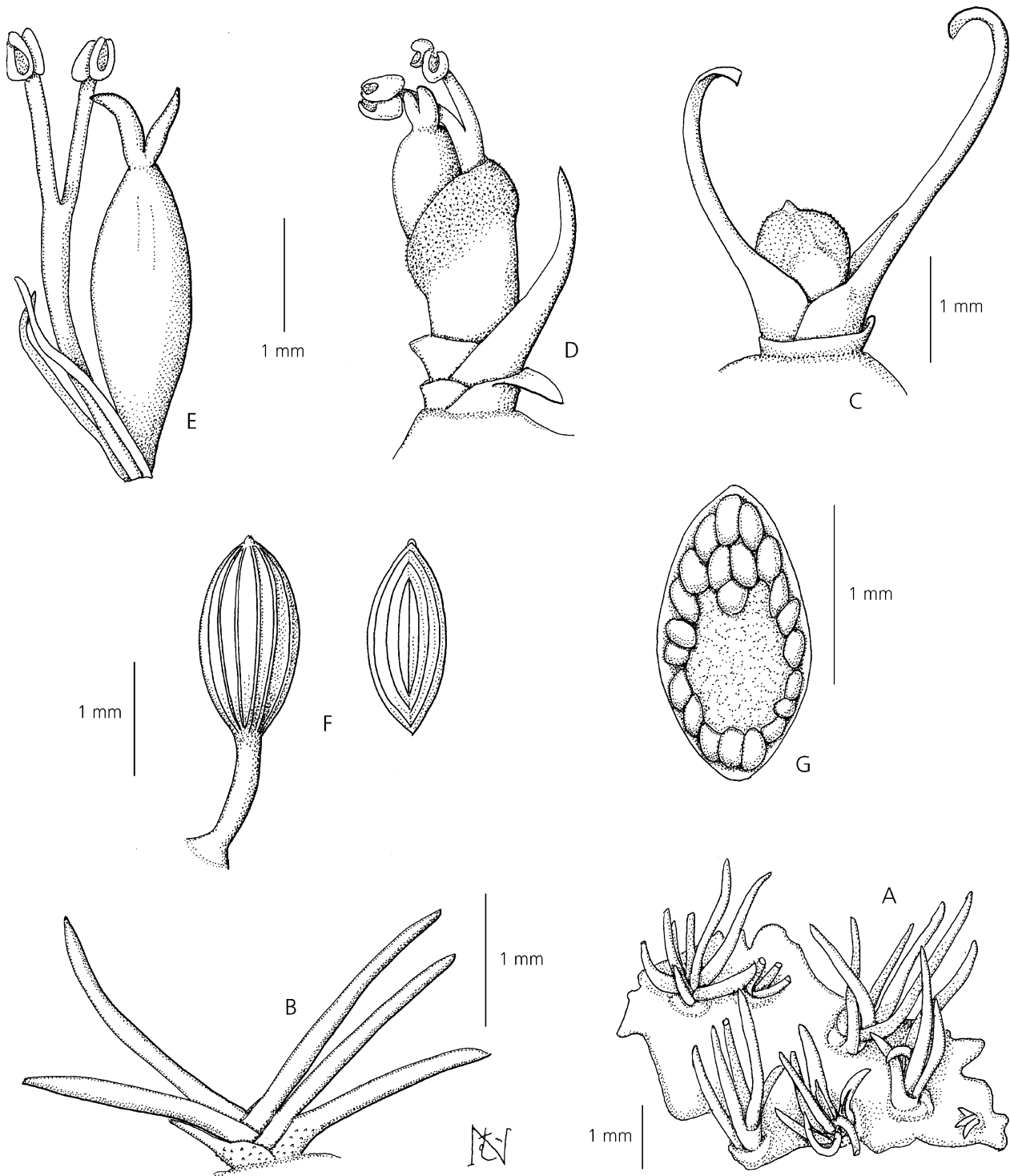


Fig. 9. *Hydrobryum tardhuangense*. **A** crustose root with tufts of leaves (i.e. vegetative shoots) on dorsal surface; **B** tuft of leaves; **C** young flower enclosed by spathe and subtended by bracts; **D** young flower with ruptured spathe and bracts; **E** flower with 1 ovary, 2 stamens on andropod and 2 tepals; **F** fruit, right, side view; **G** ovules on ovary septum with central sterile area. From *S. Koi et al.* LK-113. DRAWN BY M. NAKAJIMA.

SPECIMENS EXAMINED. LAOS. Vientiane prov.: Tad Hum waterfall, 200 m alt., 18°10'24.0"N, 102°24'55.5"E, fl. fr. Jan., *M. Kato et al.* L-01; Hinkhanna waterfall, 200 m alt., 18°03'28.0"N, 102°28'29.7"E, fl. fr. Jan., *M. Kato et*

al. L-02; *loc. cit.*, *N. Fukuoka & H. Koyama* L-65098 (type); *loc. cit.*, fl. fr. Dec., *S. Koi & T. Wongprasert* LK-08; Tad Chan Thevoda waterfall, Phuu Khao Khouay National Park, 200 m alt., 18°17'52.4"N, 102°45'10.6"E,

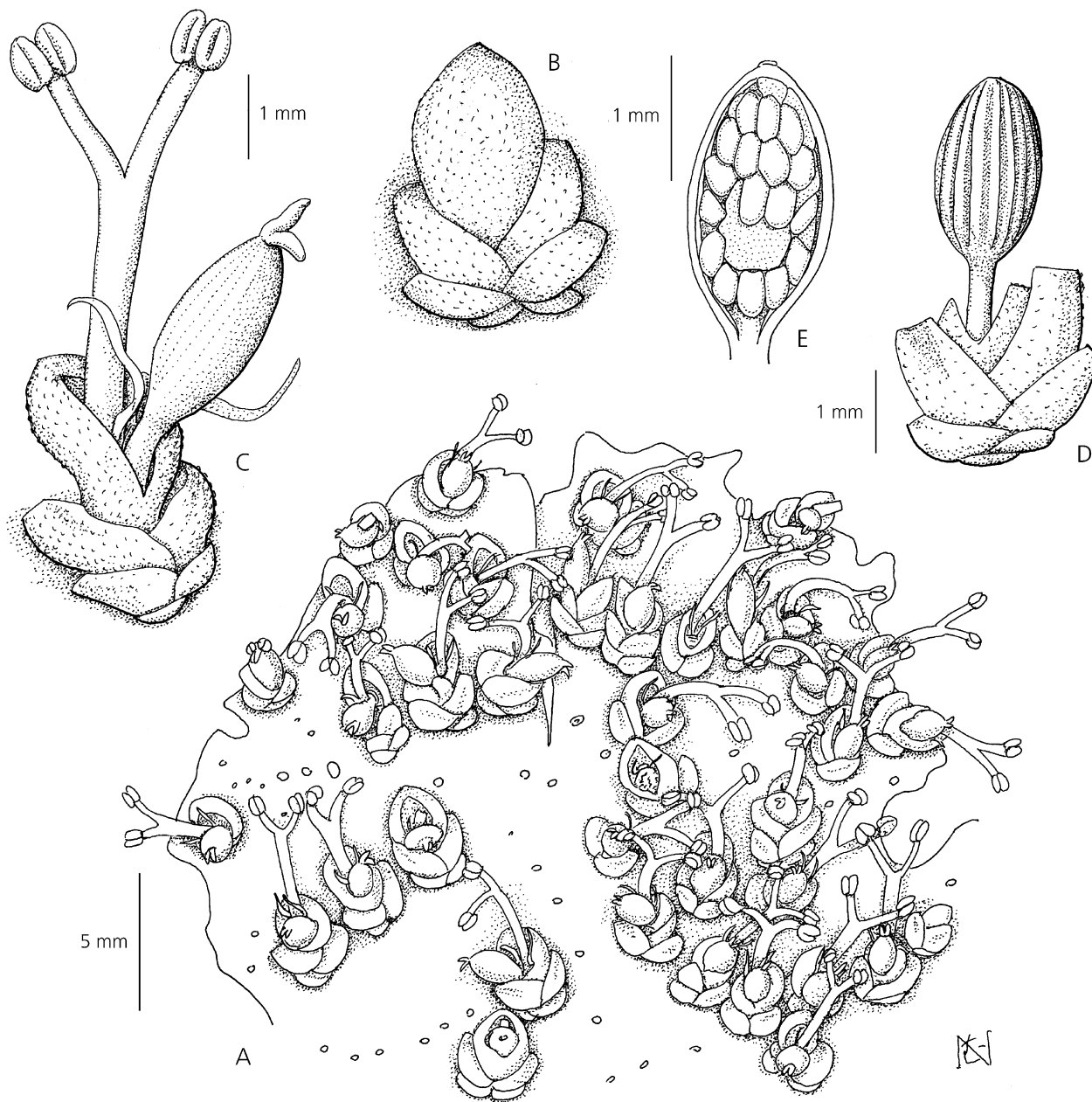


Fig. 10. *Hydrobryum vientianense*. A crustose root with flowering shoots on dorsal surface; B young flower enclosed by spathella and subtended by bracts; C flower with 1 ovary, 2 stamens on andropod and 2 tepals, protruding from ruptured spathella subtended by bracts; D fruit with ruptured spathella and bracts; E ovules on ovary septum with lower central sterile area in capsule with valve removed. From *M. Kato et al.* L-02. DRAWN BY M. NAKAJIMA.

fl. fr. Jan., *M. Kato et al.* L-16; Tad Palay waterfall, 100 m alt., fl. fr. Dec., *S. Koi & T. Wongprasert* LK-06; Tad Moun waterfall, 100 m alt., fl. fr. Dec., *S. Koi & T. Wongprasert* LK-07.

HABITAT. Epilithic on seasonally submerged rocks in waterfalls and rapids in open places.

CONSERVATION STATUS. Near threatened (NT); collected from a few spots.

NOTES. Variable in the sizes of the tepal, the filament on the andropod, the ovary, and the stigma. The spathellas split usually longitudinally at anthesis, but in

specimen *M. Kato* L-01, it is apt to rupture near the apex rather than longitudinally. The proportion of andropod to stamen is also variable within the species. The stamens mostly are branched at the middle in specimens *N. Fukuoka & H. Koyama* L-65098, *M. Kato et al.* L-01 and L-02, while branched $\frac{1}{3}$ – $\frac{1}{5}$ from the tip in specimen *M. Kato et al.* L-16.

This species is the most similar to *Hydrobryum* (= *Diplobryum*) *minutale* of southern Vietnam (newly combined below) and *H. verrucosum* of Laos in the crustose roots, 3 – 6 bracts, spathellas longitudinally

split at anthesis, flowers protruding from the spathe by elongation of ovary-stalks, and capsules up to 18 – 20-ribbed, but differs from *H. minutale* in having larger flowers (tepals, stamens and ovaries) and linear stigmas (vs capitate in *H. minutale*), and from *H. verrucosum* in the absence of projections, smaller ovaries and capsules, and having fewer ovules (8 – 27 vs 17 – 67 in *H. verrucosum*). The capsule-stalk is usually straight, not bent as described in a previous study (Kato & Fukuoka 2002). *H. vientianense* belongs to a different clade from *H. verrucosum*.

Hydrobryum vientianense is sister to *H. loeicum* of NE Thailand with which it shares most of their characters, but differs in the longitudinally dehiscent spathe (vs irregularly dehiscent in *H. loeicum*), the length of the ovary-stalk (1 – 1.5 mm vs 0.5 mm), the number of ovules (8 – 27 vs 4 – 7 per locule) and the disposition of ovules (marginal and central vs marginal) (Kato 2004). However, specimen M. Kato *et al.* L-01 has ovules either on the central and marginal parts of the placenta, or only on the marginal surface. *H. vientianense* belongs to the same clade as NE Thai *H. phetchabunense* M. Kato & Koi, but differs from it in the even surface of the root around tufts of leaves (vs raised in *H. phetchabunense*), papillate spathe (vs smooth) and a greater number of ovules (8 – 27 vs 4 – 8 per locule).

8A. *Hydrobryum minutale* (C. Cusset) Koi & M. Kato **comb. nov.** Type: Southern Vietnam (Lang Bian), Chevalier 30946bis (P!). Endemic to southern Vietnam.

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Diplobryum minutale C. Cusset, *Adansonia*, Ser. 2, 12: 279, pl. 1 (1972); Cusset (1973a: 70, pl. 11); Cusset (1992: 49).

9. *Hydrobryum austrolaoticum* Koi & M. Kato **sp. nov.** *Hydrobryum micrantheri* ovario 1-loculato, stamine singularis simile, sed capsulis pauciori-costatis differt. Typus: Laos, Champasak prov., Houay Champy river at the point crossing Route 20, 200 m alt., 15°15'30.6"N, 105°55'59.5"E, S. Koi, R. Fujinami & T. Wongprasert LKF-104 (holotypus TNS!; isotypus BKF!).

<http://www.ipni.org/urn:lsid:ipni.org:names:77120303-1>

Roots crustose, irregularly lobed; leaves 1 – 2 (or more) per tuft, linear, (0.8 –) 2 – 3.5 mm long, scattered on dorsal surface of root. Flowering shoots scattered on dorsal surface of root, solitary, appressed, flowers oblique; bracts 2 – 6 in 2 files, uniform, ovate, entire, apex obtuse, 0.5 – 1.2 mm long, smooth; spathe enclosing young flower, ellipsoidal, flattened, 1 – 1.5 mm long,

smooth, ruptured longitudinally or irregularly on dorsal surface near apex at anthesis, persistent; flowers sessile; tepals 2, on each side of stamen, linear, distal part is broader than proximal, 1 – 2.5 mm long; stamens 1, 2 – 5 mm long, longer than pistil; anthers elliptic, c. 0.3 mm long; ovaries single, stalked (stalks 0.3 – 1 mm long), unilocular, ellipsoidal, flattened, 1 – 1.6 mm long, 0.7 – 0.9 mm wide, 0.5 – 0.6 mm thick; stigmas 2, forked above base, linear to subulate, entire, equal, 0.3 – 0.8 mm long; ovules 13 – 67 per ovary, borne on whole placenta surface except in central lower area or only on marginal surface of placenta; capsule-stalks 0.7 – 1.2 mm long, capsules ellipsoidal, flattened, 1.2 – 2 mm long, 0.7 – 1 mm wide, 0.5 – 0.7 mm thick, 14 – 16-ribbed, dehiscent by 2 equal valves. Fig. 11.

DISTRIBUTION. Endemic to southern Laos.

SPECIMENS EXAMINED. LAOS. Salavan prov.: Tad Lo waterfall, 350 m alt., 15°31'36.1"N, 106°16'22.3"E, st. Jan., S. Koi *et al.* LKF-115. Champasak prov.: Tham Champee waterfall, 936 m alt., 15°12'12.5"N, 106°07'59.2"E, fl. fr. Jan., S. Koi *et al.* LK-116; Tat Yuang waterfall, 957 m alt., 15°10'50.4"N, 106°08'18.8"E, fl. fr. Jan., S. Koi *et al.* LK-122; stream in front of Laos Army Camp 16 on Route 16, 1057 m alt., 15°18'58.1"N, 106°20'09.1"E, fl. fr. Jan., S. Koi *et al.* LK-125; Houay Champy R. at the point crossing Route 20, 200 m alt., 15°15'30.6"N, 105°55'59.5"E, fl. fr. Jan., S. Koi *et al.* LKF-104 (type); *loc. cit.*, fl. fr. Jan., S. Koi *et al.* LKF-106.

HABITAT. Epilithic on seasonally submerged rocks in waterfalls and rapids in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a few spots.

NOTES. The single stamen and the unilocular ovary are common among the crustose species such as *Hydrobryum austrolaoticum*, *H. micrantherum* and *H. takakioides*, and the subcylindrical-rooted *H. subcylindricum* also has both characters. But *H. austrolaoticum* is distinct from *H. micrantherum* in a fewer capsule-ribs (vs 12 – 14 in *H. micrantherum*) and from *H. takakioides* in the very short flowering shoot and flat bract. The phylogeny shows that the similarity of *H. austrolaoticum* and *H. micrantherum* is an analogy. *H. austrolaoticum* is sister to a clade comprising *H. somranii* of NE Thailand, *H. takakioides*, *H. verrucosum* and *H. subcrustaceum* with crustose roots, and *H. taeniatum*, *H. subcylindricum* and *H. ramosum* with ribbon-like or subcylindrical roots. All but *H. verrucosum* and *H. ramosum* share the unilocular ovary (Table 1).

Specimens Koi *et al.* LK-116 and LK-125 are slightly different from the other specimens in the number and disposition of ovules; 13 – 30 ovules are borne only on the marginal surface of the placenta in the former (exceptionally a few more ovules are borne on the central upper area), whereas 25 – 67 ovules are borne on the whole placenta surface except the central lower area. Specimen Koi *et al.* LK-122 has spathe rup-

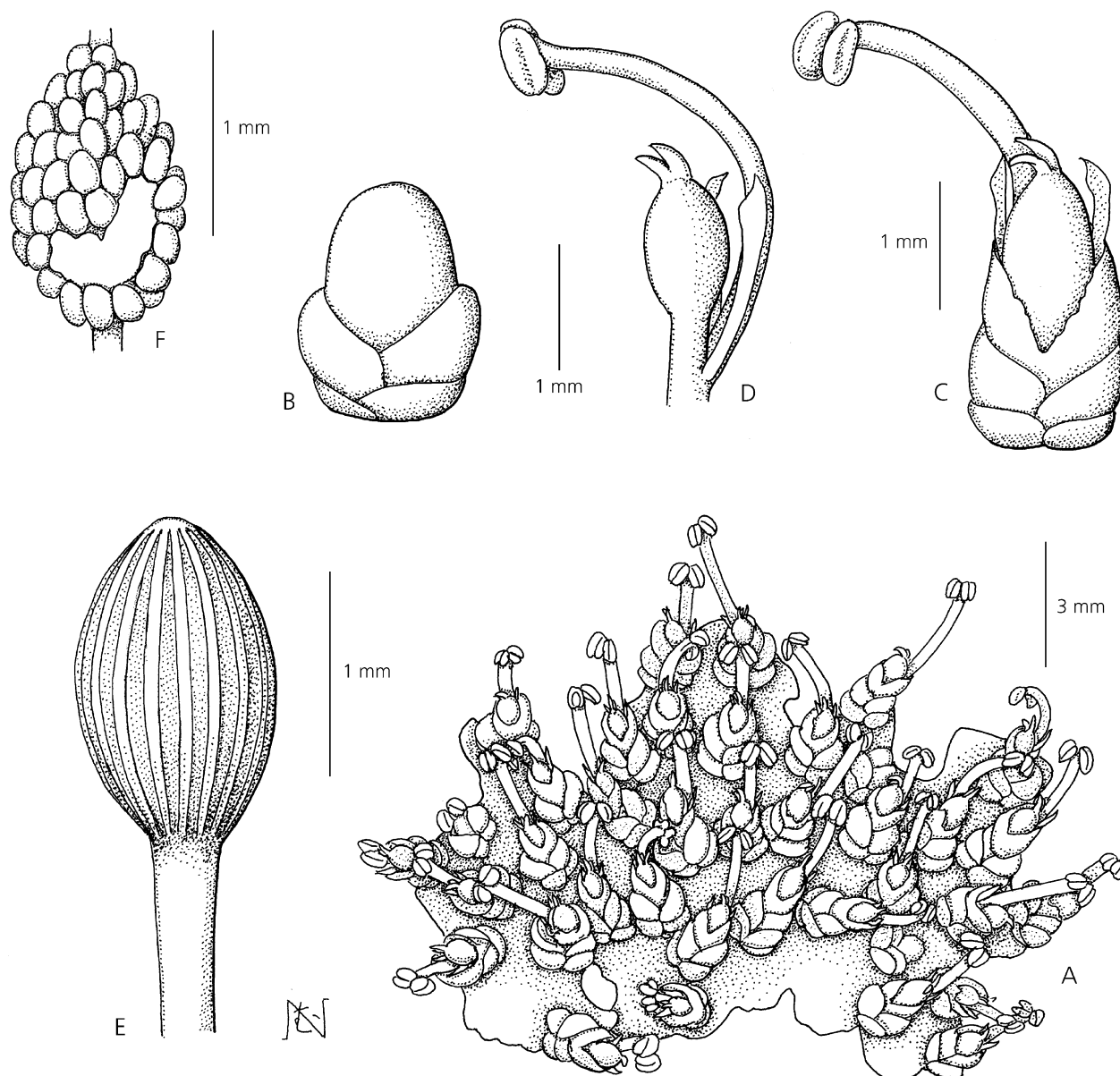


Fig. 11. *Hydrobryum austrolaoticum*. A crustose root with flowering shoots on dorsal surface; B young flower enclosed by spathe and subtended by bracts; C flower with 1 ovary, 1 stamen and 2 tepals, partly enclosed by ruptured spathe and subtended by bracts, dorsal view; D flower, side view; E capsule with 7 – 8 ribs per valve; F ovules on placenta with lower sterile area, taken out of unilocular ovary. From S. Koi *et al.* LKF-104. DRAWN BY M. NAKAJIMA.

tured irregularly on the dorsal surface and some of them have fewer ribs on the capsule. Specimen Koi *et al.* LKF-106 is abnormal though the *matK* sequence is identical to the type specimens.

10. *Hydrobryum verrucosum* Koi & M. Kato sp. nov.
H. somranii floribus erectis, setis capsularum longis simile et affine, sed radice inferne verrucosa, ovaris 2-ocularibus, ovulis plumi, capsulis pluricostatis differt. Typus: Laos, Bolikhamsai prov., Tad Xai waterfall, Phuu Khao Khouay National Park, 300 m alt., 18°27'07.0"N, 103°08'39.5"E,

M. Kato, S. Koi, C. Tsutsumi, N. Katayama, T. Wongprasert & S. Suddee L-12 (holotypus TNS!; isotypus BKF!).

<http://www.ipni.org/urn:lsid:ipni.org:names:77120304-1>

Roots crustose, irregularly lobed, adhering to rock surface by warty projections (holdfasts) scattered on ventral side; leaves 2 – 4 (or more) per tuft, 1.5 – 3 mm long or longer, linear, scattered on dorsal surface of root. *Flowering shoots* scattered on dorsal surface of root, solitary, appressed, flowers erect; bracts 3 – 6 in 2 files, uniform but basal ones smaller, ovate, entire,

apex obtuse, 1 – 1.5 mm long, papillate in marginal part; spathella enclosing young flower, ellipsoidal, flattened, 2 – 2.5 mm long, papillate except in centre, split longitudinally on dorsal surface at anthesis, persistent; pedicels 0.5 – 2 mm long; tepals 2, on each side of stamen, linear, 1.5 – 4 mm long; stamens 2 with flattened andropod, forked $1/4 - 1/8$ from tip, 4 – 8 mm long, as long as, or longer than, pistil; anthers elliptic, 0.5 – 1 mm long; ovaries single, stalked (stalks 0.7 – 2 mm long), 2-locular, ellipsoidal, slightly flattened, 2 – 3.3 mm long, 1 – 1.5 mm wide, 0.8 – 1.2 mm thick, red-purple when fresh, protruding from spathella; stigmas 2, forked at base, linear to subulate, entire, equal, 0.5 – 2 mm long, papillate; ovules 17 – 67 per locule, borne on whole placenta surface except in central lower area; capsule-stalks 1 – 4 mm long, capsules ellipsoidal, slightly flattened, 2.5 – 3 mm long, 1 – 1.5 mm wide, 0.8 – 1.2 mm thick, (12 –) 15 – 18-ribbed, dehiscing by 2 unequal valves. Fig. 12.

DISTRIBUTION. Endemic to northern central Laos.

SPECIMENS EXAMINED. LAOS. Bolikhamsai prov.: Tad Leuk waterfall, Phuu Khao Khouay National Park, 200 m alt., 18°23'42.9"N, 103°04'17.0"E, fl. fr. Jan., *M. Kato et al.* L-07; Tad Xai waterfall, Phuu Khao Khouay National Park, 300 m alt., 18°27'07.0"N, 103°08'39.5"E, fl. fr. Jan., *M. Kato et al.* L-12 (type); *loc. cit.*, 18°27'18.8"N, 103°08'31.8"E, fl. fr. Jan., *S. Koi et al.* LKF-14; Tad Nampa waterfall, Nam Nampa R., Ban Nampa, 163 m alt., 18°30'47.7"N, 103°36'26.8"E, fl. fr. Jan., *S. Koi et al.* LK-105. Khammouan prov.: hills NW of Ban Mak Pheuang on N side of Nam Thun, 950 m alt., 17°51'47"N, 105°20'2"E, fl. Oct., *M. F. Newman et al.* LAO 708 (E).

HABITAT. Epilithic on seasonally submerged rocks in waterfalls and rapids in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a few spots.

NOTES. This is similar to north-eastern Thai *Hydrobryum somranii* in the erect flowers and long (1 – 2 mm) ovary stalks. However, there are remarkable differences: in *H. verrucosum* there are prominent warty projections on the ventral side of the root, the ovary is 2-locular (vs 1-locular in *H. somranii*), the ovules are 38 – 119 per ovary (vs 12 – 24), and the capsule is 15 – 18-ribbed (vs 12 – 14). However, the capsules of *M. F. Newman et al.* LAO 708 are 12-ribbed. *H. verrucosum* is also similar to *H. vientianense* in the erect flowers with relatively long ovary-stalks, but distinct from it in having more ovules (17 – 67 per locule vs 8 – 27 in *H. vientianense*) and the projection (presence vs absence).

The above three species belong to three different clades. Although *Hydrobryum verrucosum* and *H. ramosum* show remarkable differences in the root morphology (crustose vs floating and subcylindrical), they are sister to each other.

11. *Hydrobryum subcrustaceum* Koi & M. Kato sp. nov. *H. somranii* radicibus crustaceis, surculis floriferis brevissimis, staminibus 2, ovaries, capsulis c. 12-costalis simile et affine, sed floribus adpressis, stigmatibus longioribus (1 – 1.5 mm), ovulis plumi (usque ad 37 in loculis), differt. Typus: Laos, Vientiane prov., Nam Mang 3 Dam, Mt Phuu Khao Khouay, 750 m alt., 18°21'35.9"N, 102°48'25.3"E, *S. Koi & T. Wongprasert* LK-03 (holotypus TNS!; isotypus BKF!).

<http://www.ipni.org/urn:lsid:ipni.org:names:77120306-1>

Roots crustose, lobed irregularly or sometimes associated with shoots at sinuses; leaves a few per tuft, linear, to 3 mm long, scattered on dorsal surface of root. *Flowering shoots* scattered on dorsal surface of root, solitary, appressed; bracts 2 – 4 in 2 files, uniform but basal ones smaller, ovate, entire, sheath-like base, apex obtuse, 0.5 – 1.2 mm long, papillate; spathella enclosing young flower, ellipsoidal, flattened, 1.8 – 2.5 mm long, papillate, split near apex at anthesis (stamens and stigmas emerged from spathella, ovary embedded within spathella at anthesis), persistent; flowers sessile; tepals 2, on each side of stamen, linear, 2 – 2.5 mm long; stamens 2 with flattened andropod, forked $1/3 - 1/7$ from tip, 3 – 4 mm long, longer than pistil; anthers elliptic, 0.2 – 0.4 mm long; ovaries single, subsessile (stalks 0.1 – 0.5 mm long), unilocular, ellipsoidal, flattened, 1 – 2 mm long, c. 1 mm wide, c. 0.5 mm thick; stigmas 2, forked above base, linear, entire, equal, 1 – 1.5 mm long, papillate; ovules 18 – 36 per ovary, borne on marginal surface of placenta; capsules subsessile (stalks 0.2 – 0.4 mm long), ripened within spathella, ellipsoidal, flattened, 1.5 – 2 mm long, 0.8 – 1 mm wide, 0.5 mm thick, 12 – 16-ribbed, dehiscing by 2 unequal valved. Fig. 13.

DISTRIBUTION. Endemic to northern central Laos.

SPECIMENS EXAMINED. LAOS. Vientiane prov.: Chaova waterfall, Phuu Khao Khouay National Park, 200 m alt., 18°22'07.9"N, 102°42'13.3"E, sr. fl. fr. Jan., *M. Kato et al.* L-15; Nam Mang 3 Dam, Mt Phuu Khao Khouay, 750 m alt., 18°21'35.9"N, 102°48'25.3"E, fl. fr. Dec., *S. Koi & T. Wongprasert* LK-03 (type); *loc. cit.*, fl. fr. Jan., *S. Koi et al.* LKF-02; *loc. cit.*, fl. fr. Jan., *S. Koi et al.* LKF-04.

HABITAT. Epilithic on seasonally submerged rocks in waterfalls and rapids in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a few spots in a small area.

NOTES. This species is similar to north-eastern Thai *Hydrobryum somranii* in the crustose roots, 2 stamens, and 1-locular ovaries. But *H. subcrustaceum* differs from *H. somranii* in the number of ovules (18 – 36 vs 6 – 12 per ovary in *H. somranii*), ovary-stalks (0.1 – 0.5 mm vs 1 – 2 mm long), flowers (appressed vs erect), and stigmas (1 – 1.5 mm vs 0.3 – 0.6 mm long). Although *H. subcrustaceum* is similar to *H. loicum*, *H. Chiangmaiense* M. Kato, *H. japonicum* and *H. phetchabunense* in the crustose roots,

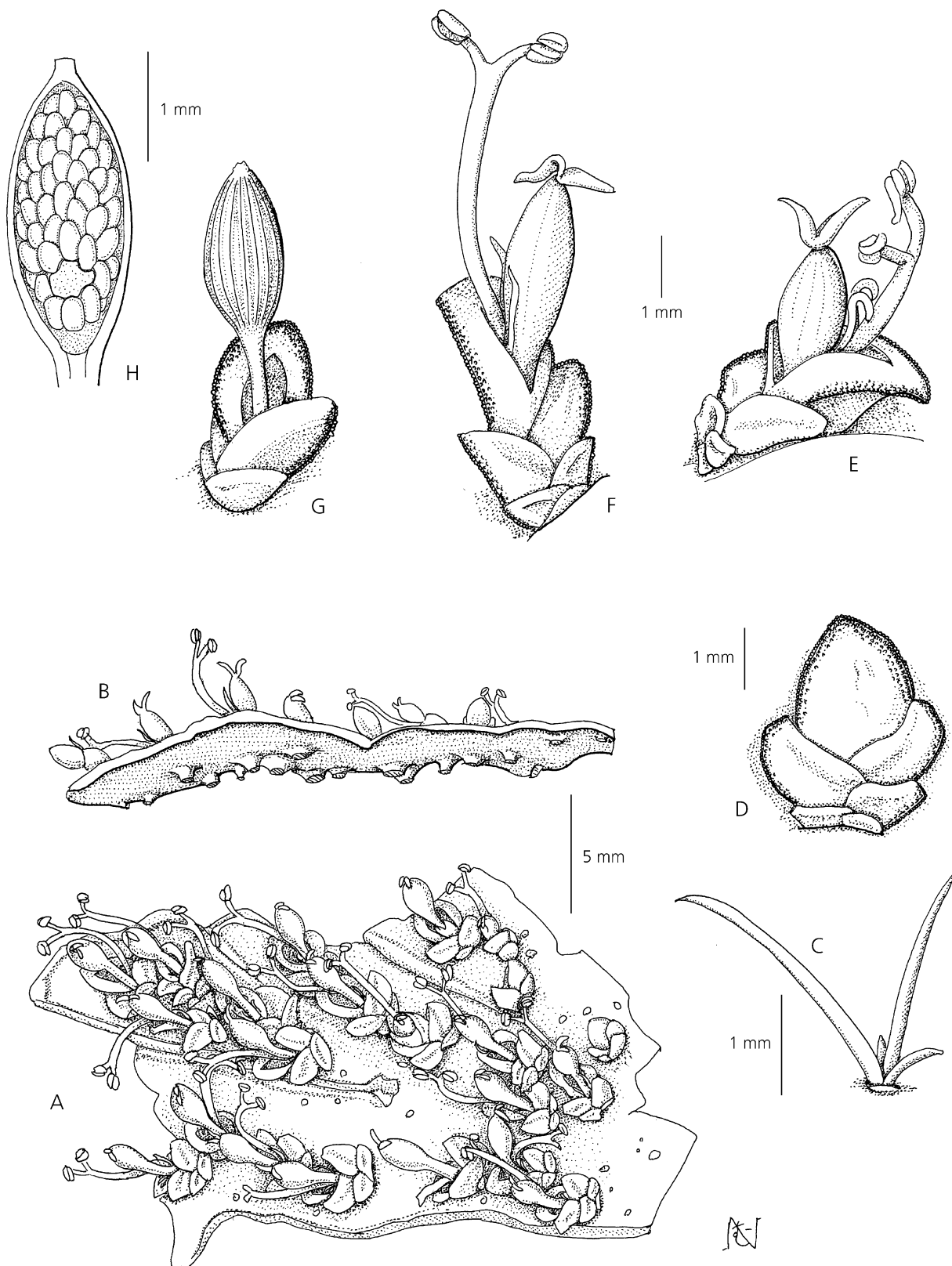


Fig. 12. *Hydrobryum verrucosum*. A crustose root with flowering shoots on dorsal surface; B side view of reproductive roots on root, showing warty projections on ventral surface; C tuft of leaves; D young flower enclosed by spathe and subtended by bracts; E young flower with ruptured spathe and bracts; F flower with 1 ovary, 2 stamens on andropod and 2 tepals, protruding from ruptured spathe and bracts; G fruit with ruptured spathe and bracts; H ovules on ovary septum with lower central sterile area in capsule with valve removed. From M. Kato et al. L-12. DRAWN BY M. NAKAJIMA.

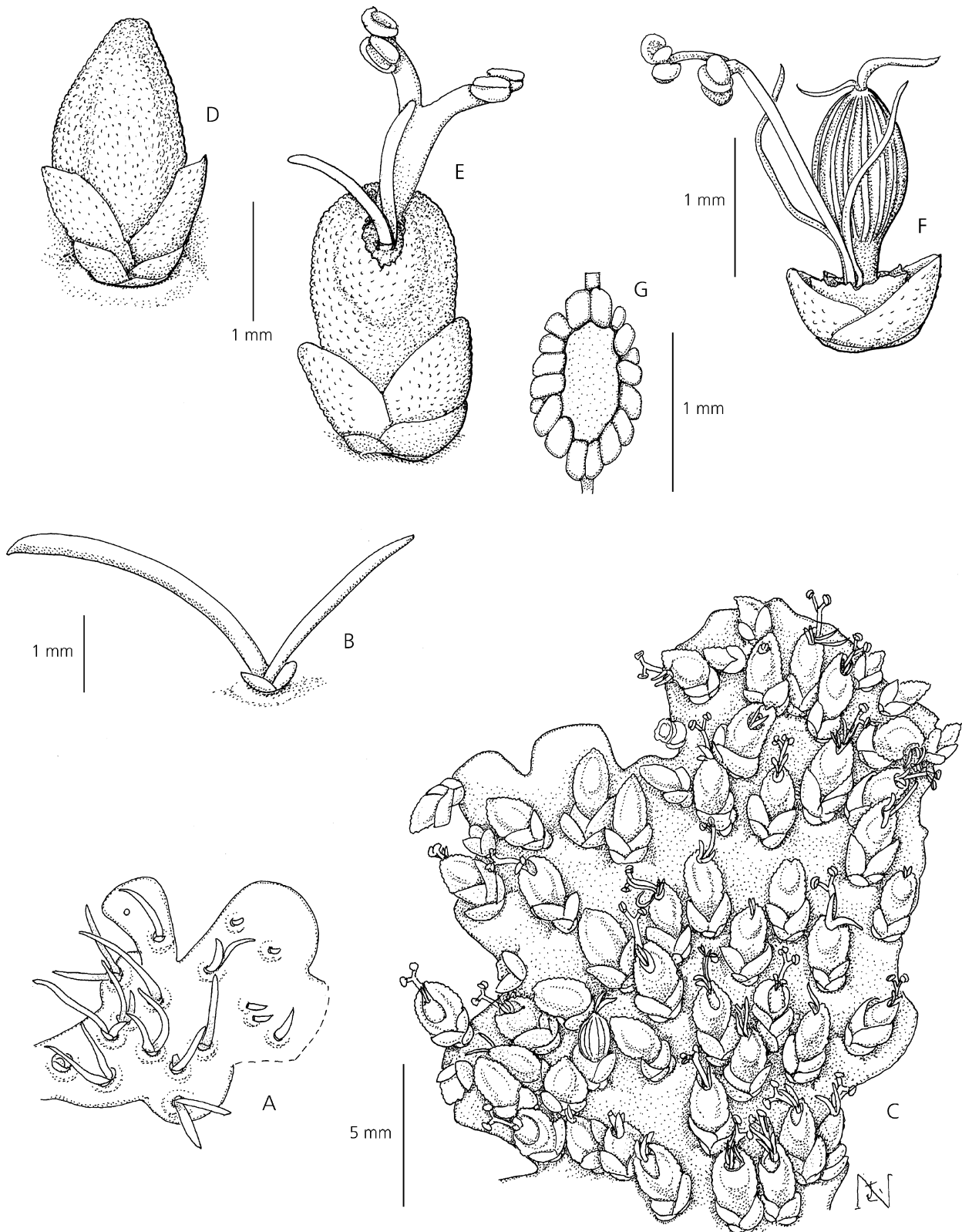


Fig. 13. *Hydrobryum subcrustaceum*. A crustose root with tufted leaves on dorsal surface; B tuft of leaves; C flowering shoots on dorsal surface of crustose root; D young flower enclosed by spathe and subtended by bracts; E flower at anthesis with ovary embedded in ruptured spathe and subtended by bracts; F young fruit with 1 capsule, 2 stamens on andropod and 2 tepals, spathe remain and bracts; G ovules on placenta with central sterile area, taken out of unilocular ovary. From S. Koi & T. Wongprasert LK-03. DRAWN BY M. NAKAJIMA.

appressed flowers, ovate bracts, linear (or entire) stigmas, and 2 stamens, it differs from these species in the number of ovary locules (1 vs 2). *H. subcrustaceum* is sister to a clade of *H. subcylindricum*, *H. takakioides* and *H. taeniatum* with subcylindrical or ribbon-like roots.

The root of *Hydrobryum subcrustaceum* is considerably lobed. Lobing is sometimes associated with shoot formation. In such an association, there are shoots on the dorsal surface interior to the sinuses between root lobes. This positional relationship between the root lobing and the shoot, though occasional, is similar to that in *Zeylanidium olivaceum* (Gardner) Engl. (Hiyama *et al.* 2002). The ribbon-like roots of *H. taeniatum* and narrowly subcylindrical roots of *H. subcylindricum* and *H. ramosum* branch always associated with shoot formation, whereas *H. austrolaoticum*, *H. somranii*, and *H. verrucosum*, like other congeners, have crustose roots being lobed without the association of shoots.

12. *Hydrobryum takakioides* Koi & M. Kato sp. nov.

Radices crustaceae, super pagina supera surculifer, a congeneris surculis floriferis 7 – 14 mm longis, bracteis (vel foliis) subulatis, separatis differt. Typus: Laos, Bolikhamsai prov., Tad Xai waterfall, Phuu Khao Khouay National Park, 300 m alt., 18°27'18.8"N, 103°08'31.8"E, S. Koi, R. Fujinami, N. Katayama & T. Wongprasert LKF-16 (holotypus TNS!; isotypus BKF!).

<http://www.ipni.org/urn:lsid:ipni.org:names:77120307-1>

Roots crustose; leaves more than 10 per tuft, linear, to 10 mm long, scattered on dorsal surface of root. *Flowering shoots* scattered on dorsal surface of root, solitary, elongated, erect, 7 – 14 mm long; bracts 22 – 34 in 6 – 7 indistinct orthostichous files, spaced, uniform, subulate, 2 – 3.5 mm long; spathella enclosing young flower, ellipsoidal, 2 – 3 mm long, papillate, ruptured irregularly at apex at anthesis, persistent; flowers sessile; tepals 2, on each side of stamen, linear, 2.5 – 5 mm long; stamen 1, 8 – 10 mm long, longer than pistil; anthers elliptic, 1 – 1.5 mm long; ovaries single, stalked (stalks 0.7 – 2.5 mm long), unilocular, ellipsoidal, 1.2 – 2 mm long, 0.5 – 0.8 mm wide, protruding from spathella; stigmas 2, forked above base, linear, entire, equal, 1 – 1.2 mm long; ovules 20 – 45 per ovary, borne on whole placenta surface, sometimes except in central lower area; capsule-stalks 1 – 2 mm long, capsules ellipsoidal, slightly flattened, 1.8 – 2.5 mm long, 0.5 – 1.2 mm wide, 0.5 – 1 mm thick, 15 – 17-ribbed, dehiscing by 2 equal valves, ribs indistinct. Fig. 14.

DISTRIBUTION. Endemic to northern central Laos.

SPECIMENS EXAMINED. LAOS. Bolikhamsai prov.: Tad Xai waterfall, Phuu Khao Khouay National Park, 300 m alt., 18°27'18.8"N, 103°08'31.8"E, fl. fr. Jan., M. Kato *et al.* L-14; *loc. cit.*, st. fl. fr. Feb., S. Koi & T. Wongprasert LK-202; *loc. cit.*, fl. fr. Jan., S. Koi *et al.* LKF-16 (type).

HABITAT. Epilithic on seasonally submerged rocks in waterfall in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a single waterfall.

NOTES. This species is remarkable in the genus for its elongate erect reproductive shoots with spaced subulate bracts and nearly radial ellipsoidal ovaries. In the reproductive shoot morphology, it looks like the unique moss *Takakia* S. Hatt. & Inoue. Phylogenetically it is related to *Hydrobryum subcylindricum* and *H. taeniatum* with subcylindrical or ribbon-like roots and very short flowering shoots.

13. *Hydrobryum taeniatum* Koi & M. Kato sp. nov.

A congeneris radibus taeniatis, a *H. subcylindrico* radibus latioribus (c. 2 mm), staminibus 2 differt. Typus: Laos, Bolikhamsai prov., Tad Leuk waterfall, Phuu Khao Khouay National Park, 200 m alt., 18°23'42.9"N, 103°04'17.0"E, M. Kato, S. Koi, C. Tsutsumi, N. Katayama, T. Wongprasert & S. Suddee L-08 (holotypus TNS!; isotypus BKF!).

<http://www.ipni.org/urn:lsid:ipni.org:names:77120308-1>

Roots ribbon-like, (1 –) 1.8 – 2 mm wide, isotomously (or anisotomously) branched, adhering to rock surface by warty projections (holdfasts) scattered on ventral side. *Flowering shoots* on dorsal surface of root at sinuses of root branching, solitary, appressed; bracts 2 – 4 in 2 files, uniform but basal ones smaller, ovate, entire, apex obtuse or sometimes acute, (0.5 – 1) c. 2.5 mm long; spathella enclosing young flower, ellipsoidal, 1.2 – 1.5 (– 1.8) mm long, slightly papillate, ruptured irregularly or longitudinally on dorsal surface near apex at anthesis, persistent; tepals 2, on each side of stamen, linear, 1.5 – 2 mm long; stamens 2 with andropod, forked to $\frac{1}{3}$ from tip, (1.5 –) c. 3 mm long, longer than pistil (or as long as pistil); anthers elliptic, 0.5 – 0.7 mm long; ovaries single, stalked (stalks to 0.2 mm long), unilocular, ellipsoidal, flattened, 0.9 – 1.2 mm long, 0.6 – 0.9 mm wide, 0.5 – 0.7 mm thick; stigmas 2, forked above base, linear, entire, equal, 0.5 – 1 mm long; ovules 20 – 27 (– 33) per ovary, borne on marginal surface of placenta; capsule-stalks c. 0.2 mm long, capsules ellipsoidal, flattened, 1.1 – 1.5 mm long, 0.9 – 1 mm wide, 0.5 – 0.8 mm thick, (15 –) 16 – 17-ribbed, dehiscing by 2 unequal valves. Fig. 15.

DISTRIBUTION. Endemic to northern central Laos.

SPECIMEN EXAMINED. LAOS. Bolikhamsai prov.: Tad Leuk waterfall, Phuu Khao Khouay National Park, 200 m alt., 18°23'42.9"N, 103°04'17.0"E, fl. fr. Jan., M. Kato *et al.* L-08 (type); Tad Nampa waterfall, Nam Nampa R., Ban Nampa, 163 m alt., 18°30'47.7"N, 103°36'26.8"E, fl. fr. Jan., S. Koi *et al.* LK-107.

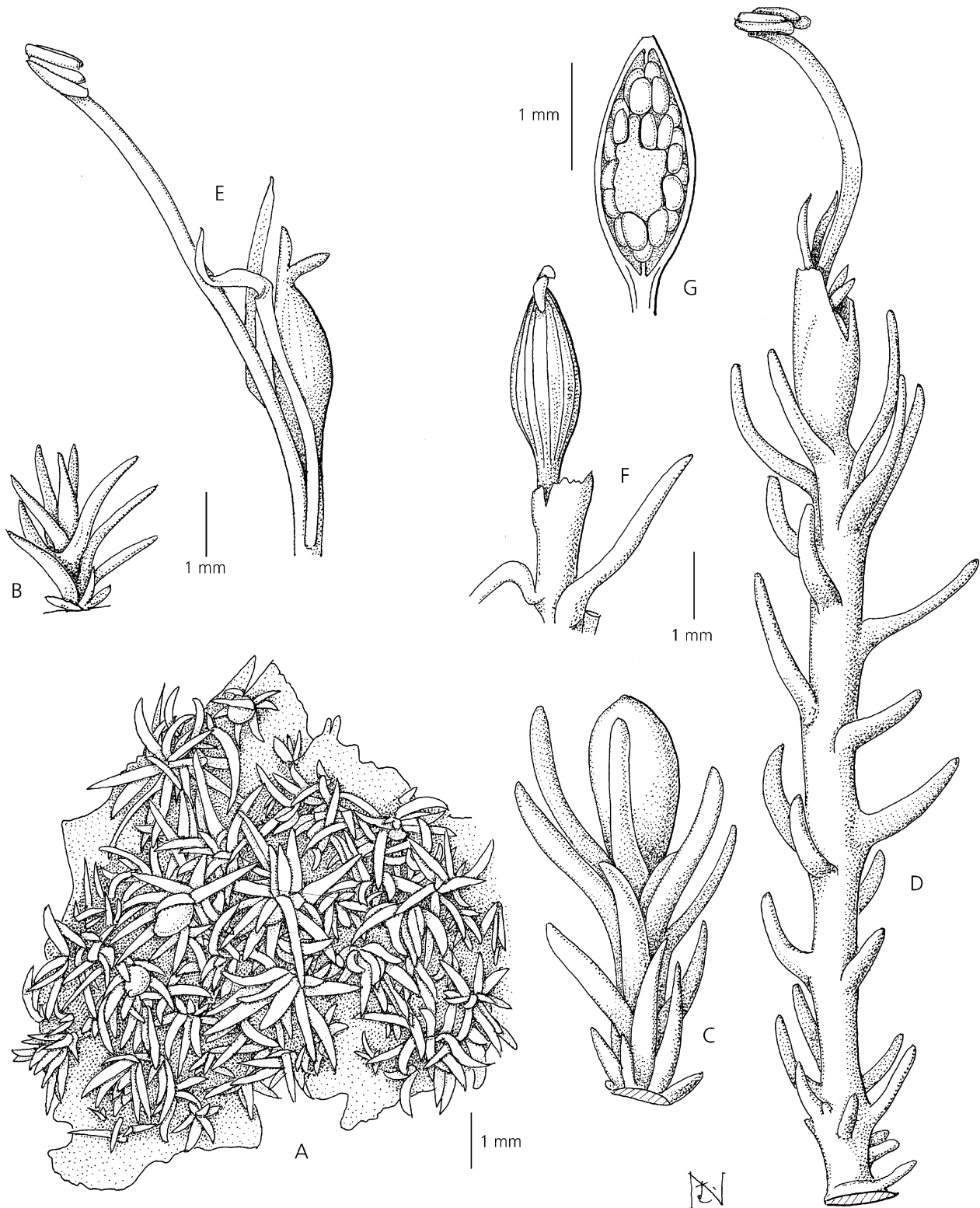


Fig. 14. *Hydrobryum takakioides*. A crustose root with vegetative shoots on dorsal surface; B vegetative shoot; C young flower enclosed by spathe at shoot tip; D shoot with flower at tip partly covered by ruptured spathe; E flower with 1 ovary, 1 stamen and 2 tepals; F young fruit with spathe remains and bracts; G ovules on placenta with central sterile area in unilocular ovary with valve removed. From S. Koi *et al.* LKF-16. DRAWN BY M. NAKAJIMA.

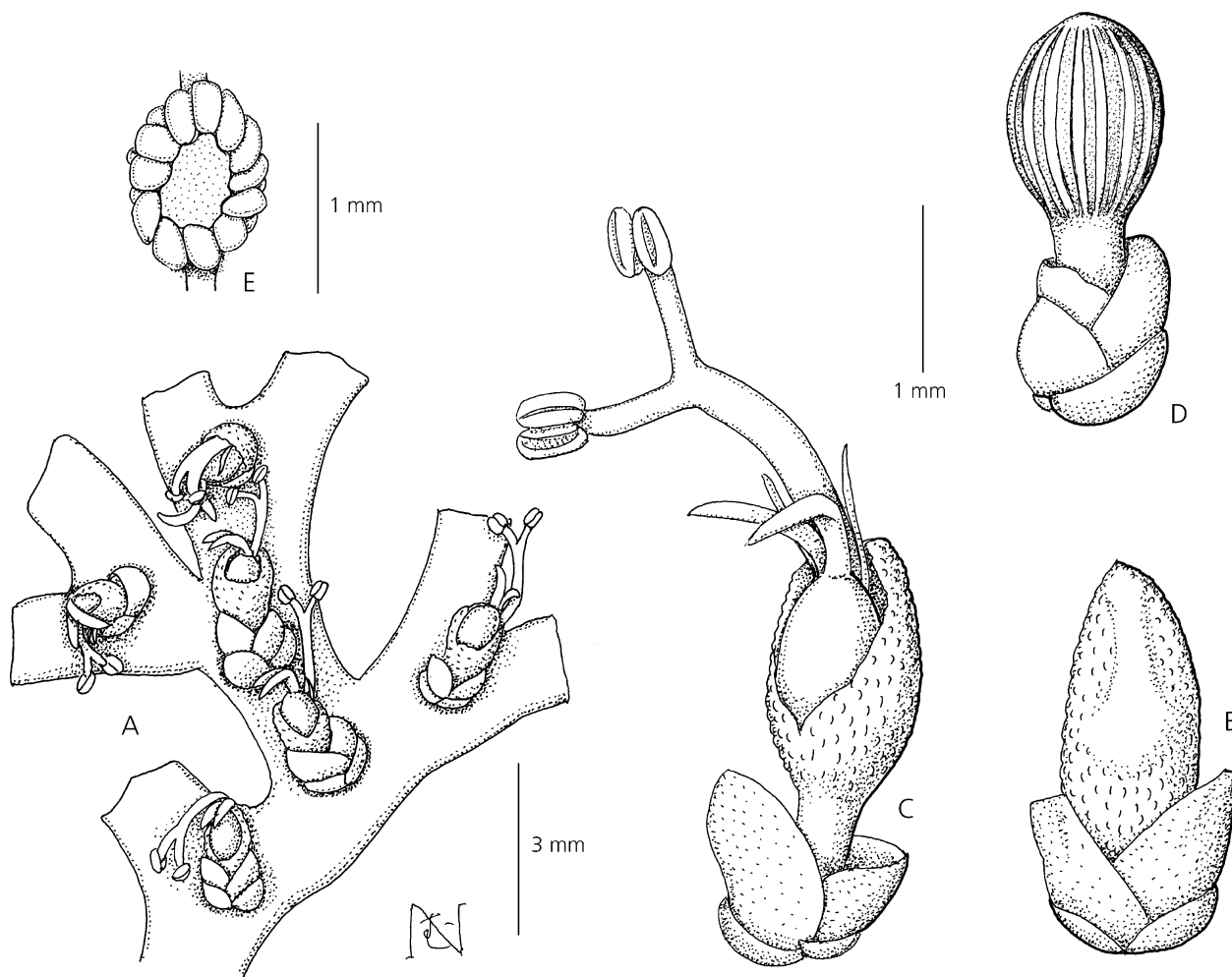


Fig. 15. *Hydrobryum taeniatum*. A ribbon-like root with flowering shoots at sinuses of root branches; B young flower enclosed by spathe and subtended by bracts; C flower with 1 ovary, 2 stamens on andropod and 2 tepals, partly protruding from ruptured spathe and subtended by bracts; D fruit with spathe remains and subtending bracts; E ovules on placenta with central sterile area, taken of unilocular ovary. From M. Kato et al. L-08. DRAWN BY M. NAKAJIMA.

HABITAT. Epilithic on seasonally submerged rocks in rapids in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a few spots in a small area.

NOTES. This is distinct from all other congeners in the ribbon-like root with shoots borne at the sinuses of root branching. In this character, *Hydrobryum taeniatum* is similar to the genera *Cladopus*, *Polypleurum* and *Zeylanidium*, but differs from *Cladopus* in the entire bracts (vs digitate in *Cladopus*), from *Polypleurum* in the appressed flower (vs erect), and from *Zeylanidium* in the 16 – 17-ribbed capsule (vs 8).

The specimen Koi et al. LK-107 is embedded in the clade of *Hydrobryum subcylindricum*. It shares all characters with M. Kato et al. L-08 except the slightly narrower root (1 – 2 mm vs 1.8 – 2 mm in L-08), longer proportion of andropod relative to stamen (forked $\frac{1}{5}$ – $\frac{1}{15}$ from tip vs $\frac{1}{3}$), and the shorter stamen (as long as pistil vs longer than pistil). *H. taeniatum* (M. Kato et al. L-08) and *H. subcylindricum* (M. Kato et al. L-09) are sympatric, suggest-

ing independence of the two species, but the relationship between them requires further analysis.

14. *Hydrobryum subcylindricum* Koi & M. Kato sp. nov. A congeneris radicibus taeniatis, a *H. taeniato* radicibus angustioribus (usque ad 1 mm), staminibus 1 differt. Typus: Laos, Bolikhamsai prov., Tad Xai waterfall, Phuu Khao Khouay National Park, 300 m alt., 18°27'18.8"N, 103°08'31.8"E, S. Koi, R. Fujinami, N. Katayama & T. Wongprasert LKF-17 (holotypus TNS!; isotypus BKF!).

<http://www.ipni.org/urn:lsid:ipni.org:names:77120309-1>

Roots creeping, adhering to rock surface by pads on ventral side, narrowly subcylindrical, 0.5 – 0.8 mm wide, isotomously branched. *Flowering shoots* on dorsal surface of root at sinuses of root branching, solitary, appressed; bracts 2 – 4 in 2 files, uniform, ovate, entire, apex acute,

0.5 – 0.8 mm long, smooth; spathella enclosing young flower, ellipsoidal with longitudinal pleat, 1.2 – 1.8 mm long, smooth, ruptured near apex at anthesis (stamens and stigmas emerged from spathella, ovary embedded within spathella at anthesis), persistent; flowers sessile (pedicels to 0.2 mm long); tepals 2, on each side of stamen, linear, 0.5 – 1 mm long; stamen 1, 2 – 2.5 mm long, as long as, or longer than, pistil; anthers elliptic, 0.2 – 0.4 mm long; ovaries single, sessile, unilocular, ellipsoidal, flattened, 0.8 – 1.2 mm long, 0.5 – 0.7 mm wide, 0.3 – 0.5 mm thick; stigmas 2, forked above base, linear, entire, equal, 0.5 – 1.2 mm long, papillate; ovules 20 – 49 per ovary, borne on marginal surface of placenta; capsules sessile (stalks to 0.2 mm long), ripened within spathella (partially emerged from torn spathella), ellipsoidal, flattened, 1.0 – 1.2 mm long, 0.8 – 0.9 mm wide, 0.5 – 0.6 mm thick, 16 – 20-ribbed, dehiscing by 2 unequal valves. Fig. 16.

DISTRIBUTION. Endemic to northern central Laos.

SPECIMENS EXAMINED. LAOS. Bolikhamsai prov.: Tad Leuk waterfall, Phuu Khao Khouay National Park, 200 m alt.,

18°23'42.9"N, 103°04'17.0"E, fl. fr. Jan., *M. Kato et al.* L-09; Tad Xai waterfall, Phuu Khao Khouay National Park, 300 m alt., 18°27'07.0"N, 103°08'39.5"E, fl. fr. Jan., *M. Kato et al.* L-13; *loc. cit.*, fl. fr. Jan., *S. Koi et al.* LKF-17 (type).

HABITAT. Epilithic on seasonally submerged rocks in waterfalls in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a few spots in a small area.

NOTES. This is similar to *Hydrobryum* (= *Diplobryum*) *ramosum* in the root being narrow-subcylindrical and the shoots borne at the sinuses of root branches, but differs in the root creeping on the rock surface (vs floating in *H. ramosum*), the single stamen (vs 2), the short ovary-stalk (0 mm vs 1 – 3.5 mm), and the unilocular ovary (vs 2-locular).

15. *Hydrobryum ramosum* (*C. Cusset*) *Koi & M. Kato comb. nov.* Type: Laos, Vientiane prov., Phu Khao Khwai (= Phuu Khao Khouay), *T. Smitinand* s.n. (C!).

<http://www.ipni.org/urn:lsid:ipni.org:names:77120310-1>

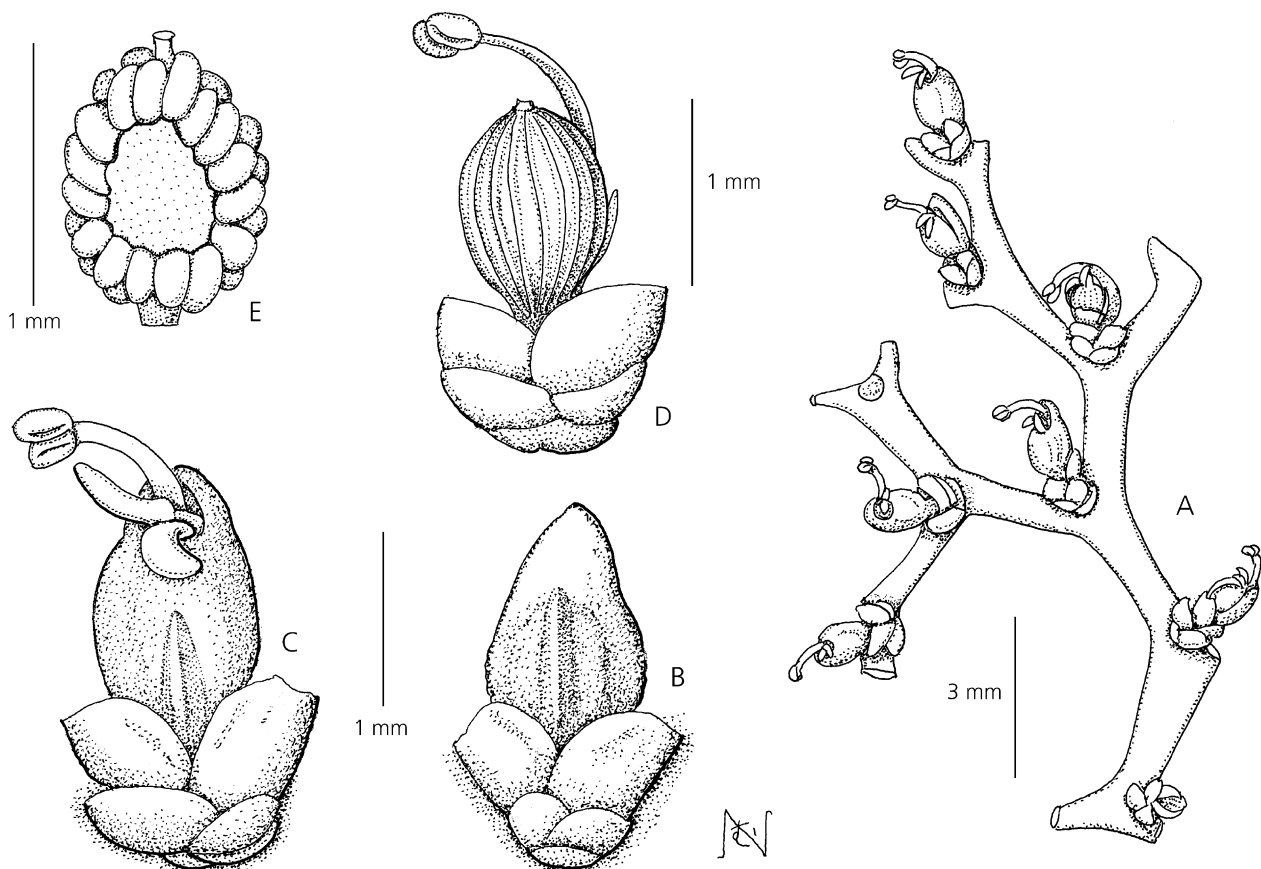


Fig. 16. *Hydrobryum subcylindricum*. A narrow ribbon-like root with flowering shoots at sinuses of root branches; B young flower enclosed by spathella and subtended by bracts; C flower at anthesis with stamen and stigmas protruding from ruptured spathella subtended by bracts; D young fruit with 1 capsule, 1 stamen and 2 tepals (1 not seen), subtended by bracts; E ovules on placenta with central sterile area, taken out of unilocular ovary. From *S. Koi et al.* LKF-17. DRAWN BY M. NAKAJIMA.

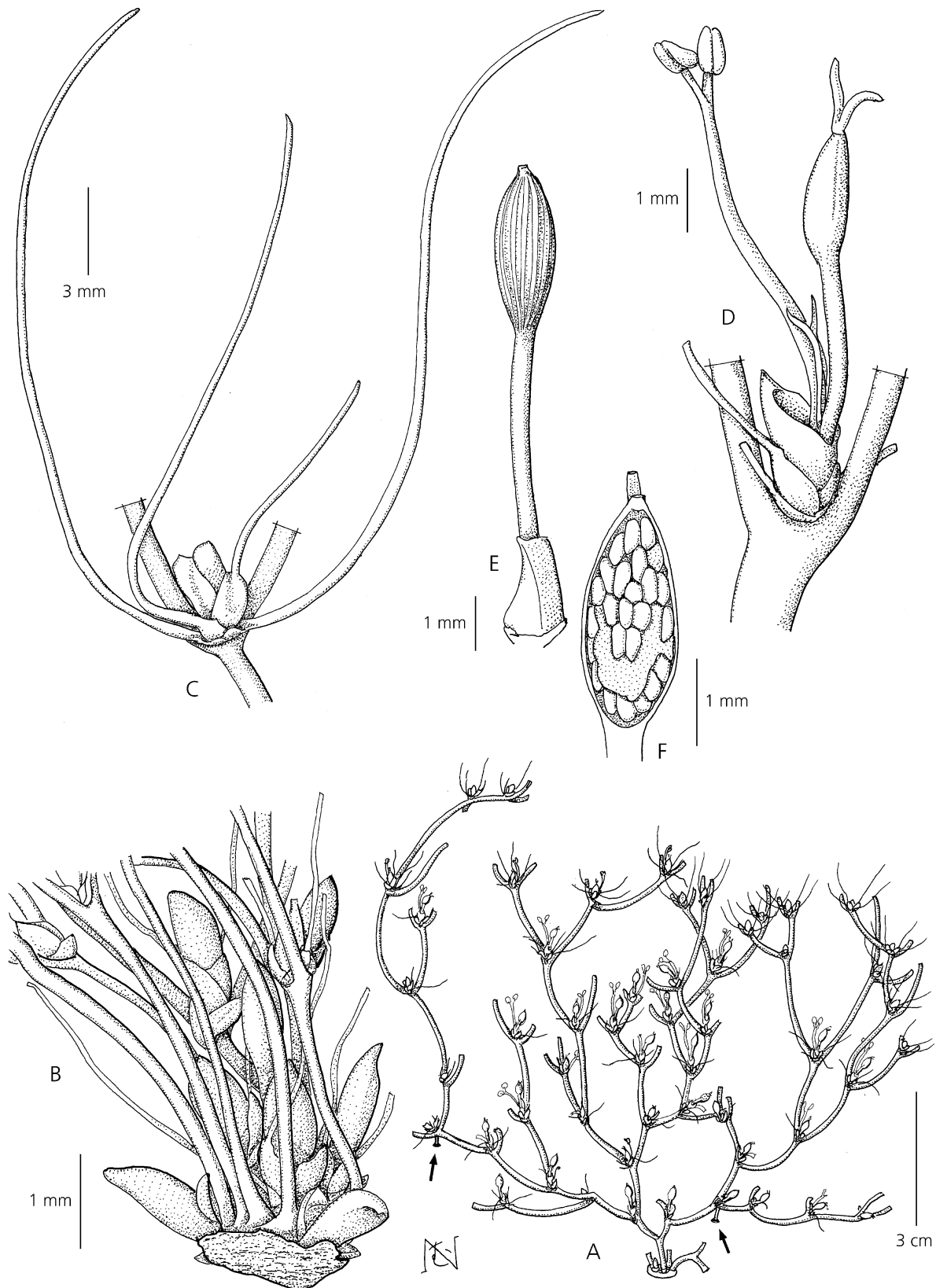


Fig. 17. *Hydrobryum ramosum*. **A** floating, narrow ribbon-like root with flowering shoots at sinuses of root branches, arrows indicate holdfasts; **B** disk-like base of root with flowering shoots; **C** young flower enclosed by spathe and subtended by bracts; **D** young flower with 1 ovary, 2 stamens on andropod and 2 tepals, protruding from ruptured spathe and subtended by bracts; **E** fruit; **F** ovules on ovary septum with lower central sterile area in capsule with valve removed. From *S. Koi & T. Wongprasert* LK-05. DRAWN BY M. NAKAJIMA.

Diplobryum ramosum C. Cusset, *Adansonia* 14: 50, f. 11 (1992).

Roots floating, attached to rock surface by small disk-like bases and a few elongate holdfasts, subcylindrical, flattened, 0.5 – 2.5 mm wide, isotomously branched; holdfasts cylindrical, c. 0.5 mm in diam., on ventral side of root opposite flowering shoots. Flowering shoots borne on dorsal surface of root at sinuses between root branching (or not associated with root branching), solitary, appressed; bracts 4 – 6 in 2 files, (oblong-) ovate, sheath-like base, thickened, apex linear (caducous), (1 – 2 mm) to 4.5 cm long; spathe enclosing young flower, ellipsoidal, funnel-like, 4 – 7 mm long, smooth, split longitudinally at anthesis, persistent; pedicels 1 – 2 mm long; tepals 2, on each side of stamen, linear, 3.5 – 5 mm long; stamens 2 with flattened andropod, forked $\frac{1}{3}$ – $\frac{1}{5}$ from tip, 5 – 12 mm long, as long as, or longer than, pistil; anthers elliptic, 0.8 – 1.2 mm long; ovaries single, stalked (stalks 1 – 3.5 mm long), 2-locular, ellipsoidal, flattened, 2.5 – 3.5 mm long, 1 – 1.5 mm wide, 0.8 – 1.2 mm thick; stigmas 2, forked above base, linear, entire, equal or subequal, 1.5 – 3 mm long, papillate; ovules 30 – 61 per locule, borne on whole placenta surface except in central lower area; capsule-stalks 2 – 10 mm long, capsules ellipsoidal, flattened, 2.5 – 4 mm long, 0.8 – 1.7 mm wide, 0.5 – 1.2 mm thick, (14 –) 16 – 18-ribbed, dehiscing by 2 equal valves. Fig. 17.

DISTRIBUTION. Endemic to northern central Laos.

SPECIMENS EXAMINED. LAOS. Vientiane prov.: Phu Khao Khwai, *T. Smitinand* s.n. (type, C); Mt Phu Kao Kwai (= Phuu Khao Khouay), *N. Fukoka* & *T. Koyama* L-65040 (L, TI, TNS); Nam Mang 3 Dam, Mt Phuu Khao Khouay, 750 m alt., 18°21'38.0"N, 102°48'26.3"E, fl. fr. Dec., *S. Koi* & *T. Wongprasert* LK-05; *loc. cit.*, fl. fr. Jan., *S. Koi et al.* LKF-05.

HABITAT. Epilithic on seasonally submerged rocks in rapids in open places.

CONSERVATION STATUS. Near threatened (NT): collected from a single spot.

NOTES. This is distinct in the genus *Hydrobryum* in the floating and subcylindrical roots. The root, like that of Sri Lankan *Polypleurum elongatum* (Gardner) J. B. Hall, adheres to the rock surface by the disk-like base and sometimes also by a few holdfasts. The root is apparently similar to the floating shoot with the disk-like base of *Hydrodiscus koyamae* (Koi & Kato 2010). Among the species examined, *H. ramosum* is the most closely related to the crustose *H. verrucosum*.

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Appendix

Materials used in phylogenetic analysis. Species names (in bold) are followed by localities (for some materials), vouchers, and GenBank accession numbers of *matK*.

Cladopus austrosinensis *M. Kato* & *Y. Kita* — CH-301, AB104560^b; CH-302, AB104559^b. **C. doianus** (*Koidz.*) *Koriba* — JK-Manose, AB179656^b. **C. fallax** *C. Cusset* — TL-701, AB293561^c; TL-1610, AB537378^d. **C. fukiensis** (*H. C. Chao*) *H. C. Chao* — CH-01, AB179653^b. **C. javanicus** *M. Kato* & *Hambali* — ID-02, AB066175^b. **C. nymanii** *H. A. Möller* — ID-03, AB104561^b; S-01, AB104577^b. **C. pierreii** *C. Cusset* — LK-117, AB610213^c; LK-121, AB610214^c; LK-123, AB610215^c; LK-128, AB610219^c; LK-132, AB610220^c; LK-134, AB610221^c; LK-211, AB610224^c; LK-214, AB610225^c; LK-221, AB610226^c; LK-222, AB610227^c; LK-232, AB610228^c; LK-237, AB610222^c; LK-241, AB610223^c; LKF-103, AB537379^d; LKF-109, AB610217^c; LKF-118, AB537380^d; LKF-120, AB610218^c. **C. queenslandicus** (*Domin*) *C. D. K. Cook* & *Rutish.* — AU-01, AB038199^a; *H. Akiyama* 16803, AB300702^c. **C. taiensis** *C. Cusset* — TL-101, AB048372^a. **Hanseniella heterophylla** *C. Cusset* — TL-311, AB104562^b; TL-1104, AB537388^d; Gaeng Tha Lad, Loei, Thailand, TPK-13, AB610229^c; Gaeng Gliang, Loei, Thailand, TPK-15, AB610230^c. **Hydrobryum austrolaoticum** *Koi* & *M. Kato* — LK-116, AB610232^c; LK-122, AB610233^c; LK-125, AB610234^c; LKF-104, AB537417^d; LKF-106, AB610231^c; LKF-115, AB537418^d. **Hy. bifoliatum** *C. Cusset* — TL-310, AB104564^b. **Hy. chiangmaiense** *M. Kato* — TK-07, AB537389^d; TL-65, AB537390^d; TL-422, AB537391^d; TL-423, AB048373^b; TL-424, AB537392^d; TL-428, AB537393^d; TL-429, AB104570^b; TL-801, AB537394^d. **Hy. floribundum** *Koidz.* — JK-Mae, AB104571^b. **Hy. griffithii** (*Wall. ex Griff.*) *Tul.* — CH-102, AB104568^b; TL-205, AB104569^b. **Hy. japonicum** *Imamura* — CH-101, AB104573^b; JK-01, AB038192^a; *J. Murata et al.* 041232, AB537396^d; Tard Muey waterfall, Maetakhra National Park, Mae On, Chiang Mai, Thailand, TK-01, AB610235^c; TL-415, AB537397^d; TL-420, AB537398^d; TL-427, AB537399^d; TL-1103, AB537400^b; Sapa, Vietnam, Vie-1, AB610236^c. **Hy. kaengsophense** *M. Kato* — TL-312, AB104565^b. **Hy. khaoyaiense** *M. Kato* — TK-09, AB537395^d. **Hy. koribanum** *Imamura ex Nakayama* & *Minamitani* —

JK-05, AB048374^a. **Hy. loeicum** *M. Kato* — TL-210, AB104566^b; TL-211, AB537401^d. **Hy. micrantherum** var. **crassum** *M. Kato* — TL-57, AB038205^a; TL-58, AB104574^b; TL-306, AB104576^b. **Hy. micrantherum** var. **micrantherum** (*P. Royen*) *C. D. K. Cook & Rutish.* — TL-62, AB104575^b. **Hy. phetchabunense** *M. Kato & Koi* — TKF-01, AB537414^d, TL-1102, AB537415^d. **Hy. punctulatum** *Koidz.* — JK-Yaku, AB104572^b. **Hy. ramosum** (*C. Cusset*) *Koi & Kato* — LK-05, AB537383^d; LKF-05, AB610237^c. **Hy. somranii** *M. Kato* — TL-703, AB537402^d; TL-704, AB537403^d. **Hy. subcrustaceum** *Koi & M. Kato* — L-15, AB537408^d; LK-03, AB537409^d; LKF-02, AB537410^d, LKF-04, AB537411^d. **Hy. subcylindricum** *Koi & M. Kato* — L-09, AB537405^d; L-13, AB610238^c; LKF-17, AB537406^d. **Hy. taeniatum** *Koi & M. Kato* — L-08, AB537404^d; LK-107, AB610239^c. **Hy. takakioides** *Koi & M. Kato* — L-14, AB610240^c; LK-202, AB610241^c; LKF-16, AB537407^d. **Hy. tardhuangense** *M. Kato* — LK-113, AB610242^c; TL-208, AB104567^b. **Hy. verrucosum** *Koi & M. Kato* — L-07, AB537412^d; L-12, AB610243^c; LK-105, AB610244^c; LKF-14, AB537413^d. **Hy. vientianense** (*M. Kato & Fukuoka*) *Koi & M. Kato* — L-01, AB537384^d; L-02, AB610245^c; L-16, AB537385^d; LK-06, AB537386^d; LK-07, AB610246^c; LK-08, AB537387^d; TKF-02, AB537416^d; Gok-tab waterfall, Loei, Thailand, TPK-26A, AB610247^c; *loc. cit.*, TPK-26B, AB610248^c; Gaeng Hua Wang Hai, Loei, Thailand, TPK-28, AB610249^c; Loei stream, Loei, Thailand, TPK-29, AB610250^c. **Hydrobryum** sp. — Gaeng Songkone, Loei, Thailand, TPK-01, AB610253^c. **Hydrobryum** sp. — Gaeng Wang Gohia, Loei, Thailand, TPK-16, AB610251^c. **Hydrobryum** sp. — Huai Phai waterfall, Loei, Thailand, TPK-22, AB610252^c. **Hydrodiscus koyamae** (*M. Kato & Fukuoka*) *Koi & M. Kato* — L-06, AB537381^d; L-11, AB537382^d; LK-104, AB610255^c; LKF-13, AB610254^c. **Paracladopus chanthaburiensis** *Koi & M. Kato* — TL-1533, AB293558^c. **Pa. Chiangmaiensis** *M. Kato* — LK-213, AB610258^c; LK-220, AB610259^c; LK-223, AB611703^c; LKF-105, AB610256^c; LKF-110, AB537419^d; LKF-116, AB610257^c; LKF-119, AB537420^d; LKF-121, AB537421^d; TL-808, AB293560^c; TL-1706, AB537422^d. **Polypleurum elongatum** (*Gardner*) *J. B. Hall* — SL-12, AB048376^a. **Po. erectum** *M. Kato* — Cha Naen waterfall, Phu Wua Wildlife Sanctuary, Nong Khai, Thailand, TL-706, AB610260^c. **Po. insulare** *M. Kato & Koi* — Khlong Phu waterfall, Ko Chang, Trat, Thailand, TL-1512, AB610261^c. **Po. longicaule** *M. Kato* — Tharn Ngam waterfall, Udun Thani, Thailand, TL-709, AB610262^c; *loc. cit.*, TL-901, AB610263^c. **Po. longifolium** *M. Kato* — Cha Naen waterfall, Phu Wua Wildlife Sanctuary, Nong Khai, Thailand, TL-707, AB610264^c; *loc. cit.*, TL-904, AB610265^c. **Po. longistylosum** *M. Kato* — TL-318, AB104578^b; Phoolao waterfall, Si Sa Ket, Thailand, TL-1503, AB610266^c. **Po. munnarensense** *Nagendran & Arekal* — Kuriyarkutty R., Orukomban, Parambikulam

Wildlife Sanctuary, Trichur, Kerala, India, *A. K. Pradeep* 90004, AB610267^c. **Po. phuwuansense** *M. Kato* — Chet Si waterfall, Phu Wua Wildlife Sanctuary, Nong Khai, Thailand, TL-705, AB610268^c. **Po. pluricostatum** *Koi & M. Kato* — LK-01, AB610269^c; LK-02, AB610270^c; LK-04, AB610271^c; LKF-01, AB610272^c; LKF-03, AB610273^c; Lad Hin Tak waterfall, Phu Rua National Park, Loei, Thailand, TPK-20, AB610274^c. **Po. prachinburiense** *M. Kato & Koi* — Takro waterfall, Prachinburi, Thailand, TL-1404, AB610275^c; Kaeng Hin Phoeng waterfall, Khao Yai National Park, Na Dee, Prachinburi, Thailand, TL-1601-1, AB610276^c; *loc. cit.*, TL-1602, AB610277^c; *loc. cit.*, TL-1604, AB610278^c. **Po. schmidtianum** *Warm.* — LK-106, AB610279^c; Sato stream, Klong Sato, Bo Rai, Trat, Thailand, TKF-21, AB610463^c; Saphan Hin waterfall, Trat, Thailand, TL-1303, AB610280^c; *loc. cit.*, TL-1508A, AB610281^c; *loc. cit.*, TL-1508B, AB610282^c. **Po. sisaketense** *M. Kato & Koi* — Phoolao waterfall, Kantharalak, Si Sa Ket, Thailand, TL-1502, AB610464^c. **Po. stylosum** (*Wight*) *J. B. Hall* — Kunthipuzha, Mannarkkad, Malappuram, Kerala, India, *A. K. Pradeep* 90003, AB610465^c; Panathur, Kasaragod, Kerala, India, KI-109, AB610466^c; Cheenganni Puzha, Kannur, Kerala, India, KI-211, AB610467^c; Punavoorthodu Urulanthanni, Ernakuram, Kerala, India, KI-222, AB610468^c; SL-05, AB066174^b. **Po. wallichii** (*R. Br. ex Griff.*) *Warm.* — L-03, AB610470^c; LK-09, AB610471^c; LK-127, AB610472^c; LK-238, AB610473^c; TL-55, AB038204^a; Nang Rong waterfall, Khao Yai National Park, Nakhon Nayok, Thailand, TL-601, AB610469^c. **Po. wongprasertii** *M. Kato* — TL-319, AB104579^b. **Thawatchaia trilobata** *M. Kato, Koi & Y. Kita* — TL-419, AB104563^b; Gaeng Khem, Dansai, Loei, Thailand, TPK-02, AB610474^c; Gaeng Tham, Huaylad, Dansai, Loei, Thailand, TPK-04, AB610475^c; Gaeng Tha Laad, Phu Ruea, Loei, Thailand, TPK-14, AB610476^c. **Zeylanidium lichenoides** (*Kurz.*) *Engl.* — KI-37, AB104582^b. **Z. subulatum** (*Gardner*) *C. Cusset* — Pooyam Kutty R. near Kothamanglam, Ernakuram, Kerala, India, KI-219, AB610477^c; SL-01, AB038202^a.

Sources: ^a Kita & Kato (2001), ^b Kita & Kato (2004), ^c Koi *et al.* (2008), ^d Koi & Kato (2010), ^e present study.

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