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Stories from the Mekong, part 2. The *Cryptocoryne* (Araceae) of Chiang Khan District, Loei Province, Thailand

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ABSTRACT

Between March 2006 and February 2015, the occurrence and habitats of the aroid genus *Cryptocoryne* were investigated in Chiang Khan District, Loei Province, Thailand. In addition to the well-known *Cryptocoryne crispatula* Engl. var. *crispatula* and *C. crispatula* var. *yunnanensis* (H.Li) H.Li & N.Jacobsen, a recently described species was found: *C. loeiensis* Bastmeijer *et al.*, as well as a number of plants considered to be hybrids. Although *Cryptocoryne* is presently abundant, decimation or extinction could occur in the future because of the dam constructions in the Mekong River.

KEYWORDS: *Cryptocoryne*, Araceae, habitats, hybrids, floodplain, hydro-power dam.

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INTRODUCTION

The Mekong River (Mae Nam Khong) is the longest river in Southeast Asia, running through six countries with a length of around 4,800 km and emptying into the South China Sea. Its catchments area is about 795,000 km^2, approximately about 1½ times as large as Thailand or France. The biodiversity of the Mekong River basin is only exceeded by that of the Amazon River basin, and it is one of the most productive inland fisheries in the world, with over 1300 fish species (WWF, 2008). The present study area Chiang Khan is located about 1,700 km from the estuary, at an altitude of about 200 m a.s.l. Observations were made during March–April 2006, March 2007, March 2008, January 2010, August 2010, January 2011, and February 2015.

The first part of 'Stories from the Mekong', was published by Idei *et al.* (2010) with the description of two new taxa of *Cryptocoryne*: *C. mekongensis* Idei *et al.* and *C. crispatula* var. *decus-mekongensis* Idei *et al.*, with pictures of their habitats in southern Lao P.D.R. as well as of the plants. An overview of the genus *Cryptocoryne* as well as other species mentioned in this article may be found in Jacobsen (1980), Bastmeijer (2017) and in Jacobsen *et al.* (2012) regarding their occurrence in Thailand.

Maxwell (2009), presented a survey of the vegetation and flora of the Mekong between Kratie and Stung Treng, in central Cambodia, where *Cryptocoryne crispatula* var. *crispatula* was recorded. Puff & Chayamarit (2011) presented a study of the rheophytes of the Mekong at the Pha Taem N.P., some 800 km further down the Mekong from Chiang Khan together with data from the Mekong River basin, but did not report any *Cryptocoryne*.

CLIMATE

Chiang Khan has a tropical savanna climate with an average annual temperature of about 26°C. The dry season is from November to April with an average monthly precipitation of around 16 mm, and the driest period (December and January) having total average rainfall of merely 8 mm. The rainy season is from May until September with an average precipitation of around 1100 mm per month (Climate-data, 2017).

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There is a period of relative low temperatures from December to February with a daily mean low of 15°C (frequently down to 9°C), and a daily mean high of 29°C (up to 34°C). A higher temperature period from March and April has a daily high of 34°C (frequently rising to 41°C), and a daily low of 22°C (occasionally as low as 19°C). The daily temperature range from May to September is narrower with a daily low of around 23°C (for a month mean) to daily high of around 32°C (Accuweather, 2017; Climate-data, 2017; Tempstat, 2017).

The rainfall in the upper parts of the Mekong catchments region influences the water level fluctuations more than does the local rainfall, and thus has an influence on the *Cryptocoryne* ecology in the shallow water places during the dry season. In the smaller tributaries to the Mekong the local rainfall is of more importance as regards the situation in the local habitat.

INVESTIGATION AREA

The study site is on sedimentary rock in the meandering riverbed about 35 km downstream from Chiang Khan, focused on the five areas of Chiang Khan western part, Chiang Khan eastern part, Kaeng Khut Khu (Kaeng Kood Koo), Ban Pah Baen and Ban Hat Bia; all with abundant *Cryptocoryne* populations. The width of the river varies from about 0.3 km to 1.2 km, and at Chiang Khan town, it is approximately 0.6 km wide. The open laterite soil in the steep riverbanks (Fig. 1A) and the boundary of the secondary forests clearly reveals the extent of the highest water levels (Fig. 1B), where the soft soils are often collapsing owing to river erosion during high water, and also owing to the deforestation along and around the riverbanks. The three segments in the river profile are the steeply inclined riverbank, the seasonal floodplain, which is to some extent undulated, and the channel of the perennial river. The channel of the perennial river is not braided between Chiang Khan and Pak Chom. The floodplain may amount to about 60–90% of the width of the river in the latter half of the dry season, when it has a prominent detritus cover. Local residents perform seasonal agriculture on the exposed floodplain during the dry season (Fig. 2). The sedimentary rock riverbed is overall comparatively flat, although moderately steep places do occur. Characteristics of various sedimentary rocks, such as mud rock with the slaking, slate, clastic dike, granule-cobble conglomerate, and convolute bedding, are seen frequently. Heaps of exposed large boulders, and high rocky shelves that are found elsewhere in the Mekong flood plain do not occur in the investigated area.

RIVER PROFILE

Water level: Figure 3A shows the annual water level fluctuation for selected years. The absolute water depth, is based on a zero gauge of 194 m above MSL by an official water gauge in Chiang Khan. The minimum water level is defined as 1.9 m, and floodwater level is defined as 17.4 m (Mekong River Commission, 2017; for additional data see also Puff & Chayamarit, 2011). Figure 3B–C shows the water level measurement scale at Chiang Khan on 1 January 2010.

The water level fluctuation at Chiang Khan originates from the rainfall in the upriver districts (especially in northern part of the Lao P.D.R.) rather than the local weather, and a temporary rise in water level occurs frequently even during the dry season. Furthermore, the actual water level is always fluctuating owing to ripples or small waves, and these are not reflected in daily water gauge data. When standing on the river bank one can frequently see fluctuations of more than 15 cm within a minute and this is especially notable at water levels below 4.0 m. Hydropower dams operating in the upstream of China's Yunnan Province have continuously been affecting water level fluctuations in recent years.

During the rainy season the muddy water contains soil particles and various types of driftwood and other floating fragments. Water visibility is always the less than 10 cm in August. The clearest water flow is found from the middle of March to the beginning of April, with visibility increasing to a depth of about 80 cm in the clearest parts. The seasonal surface water temperature in the mainstream varies from January (ca 22°C) to March–April (ca 29°C).

FLOODPLAIN

The floodplain is generally below the water level at 6.5 m (see Fig. 3). The soil surface emerges gradually after the middle of November with numerous ephemeral shallow rapid streams occurring on the

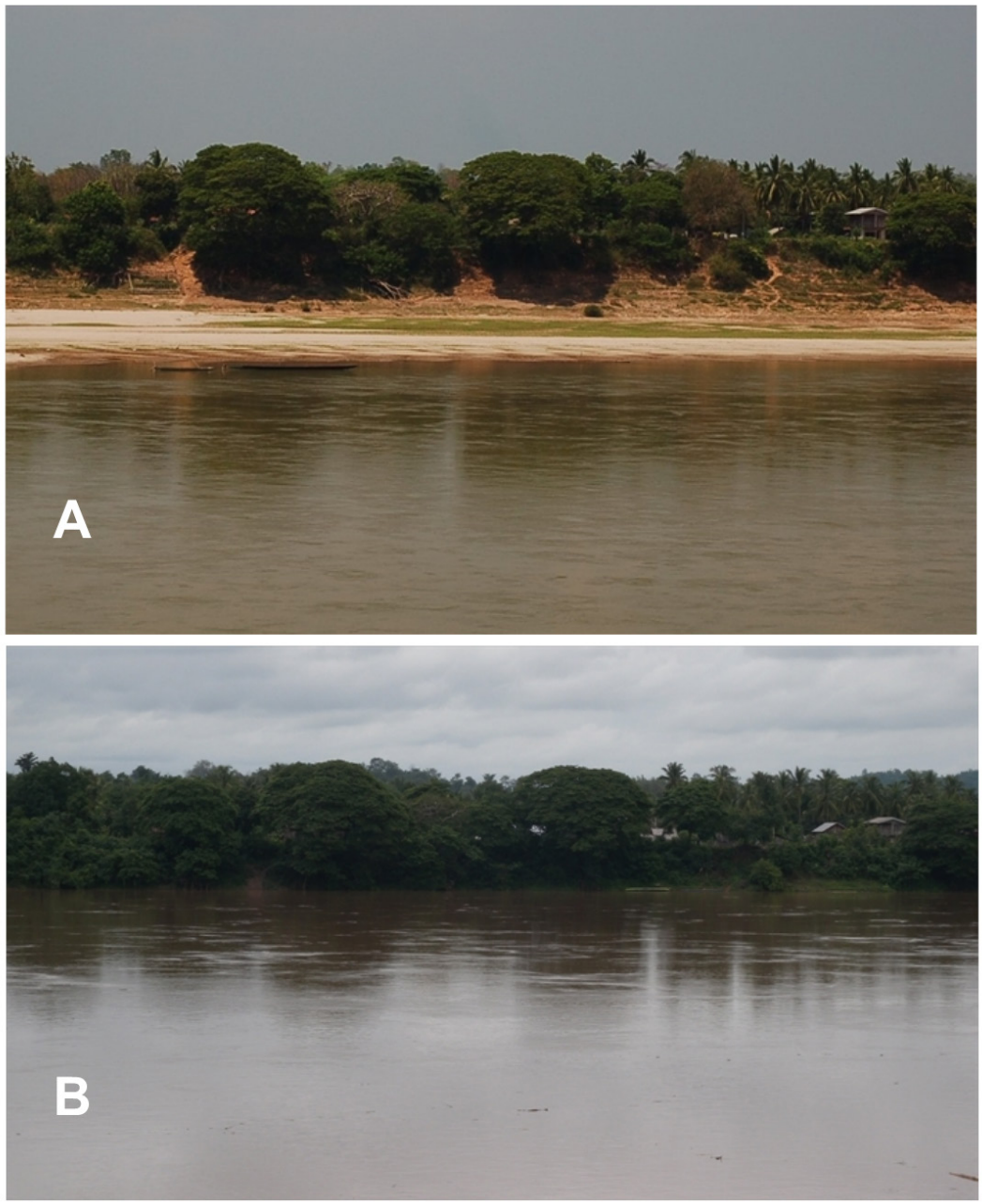

Figure 1. Seasonal water level fluctuation in front of Chiang Khan town; A. 5 April 2006, with a water level of ca 3.5 m. The bare laterite soil of the steep riverbank and the boundary of the secondary forests shows the extent of the highest water levels; B. 15 August 2010, water level ca 10.5 m. Photographs by T. Idei unless otherwise stated.

Figure 2. Seasonal agriculture on the high accumulated mobile sand at Ban Pah Baen during the dry season, 13 January 2010. The accumulated layer consists of mobile detritus; the vertical accumulation range varies from the thin layer immediate above the sedimentary rock to more than 5 m in sheltered places.

floodplain. Creeks and stagnant pools are then formed in openings on the sedimentary rock that emerges during the latter half of the dry season (Fig. 4A).

The floodplain consists of a sediment layer and a surface accumulation layer (Fig. 4B). The sediment layer is composed of an assortment of deposited detritus with stones of various sizes due to the undertow. The mixture and the vertical range varies spatially (Fig. 5). The accumulation layer consists mainly of detritus with stones; the vertical accumulation range varies from the thin accumulation immediately above the sedimentary rock, to an accumulation of more than 5 m and forming gentle undulating sandbars, which vary every year. The habitat of *Cryptocoryne* shows a considerable accumulation of plastics on the surface and down to a depth of 50 cm.

VEGETATION

The seasonal vegetation layer appears during the latter half of the dry season. The sluggish flow section is inhabited by the aquatics *Hydrilla verticillata* (L.f.) Royle, *Najas indica* (Willd.) Cham., *Potamogeton crispus* L., and *Vallisneria gigantea* Graebn. As the eastern part of Chiang Khan, located about 1 km downstream from the water gauge, an amphibious vegetation layer is situated immediately above the aquatic layer in the floodplains with a water level up to 5.5 m. Here *Cryptocoryne* is distributed in the range from water level 3.2 to 5.5 m (see Fig. 3A), and dense populations of *Cryptocoryne* are situated from water level 3.4 m to 4.0 m. In the positions higher than this, they are only found in somewhat protected habitats.

Rheophytic shrubs were not studied during our investigation, and the only species that we with some certainty can say that was found in abundance is the very widespread *Homonoia riparia* Lour. Besides shrubs, there are a number of herbaceous plants in the generally annual habitats. Puff & Chayamarit (2011) described a large number of rheophytes from the Mekong further downstream from Chiang Khan, and Maxwell (2009) described the comparable

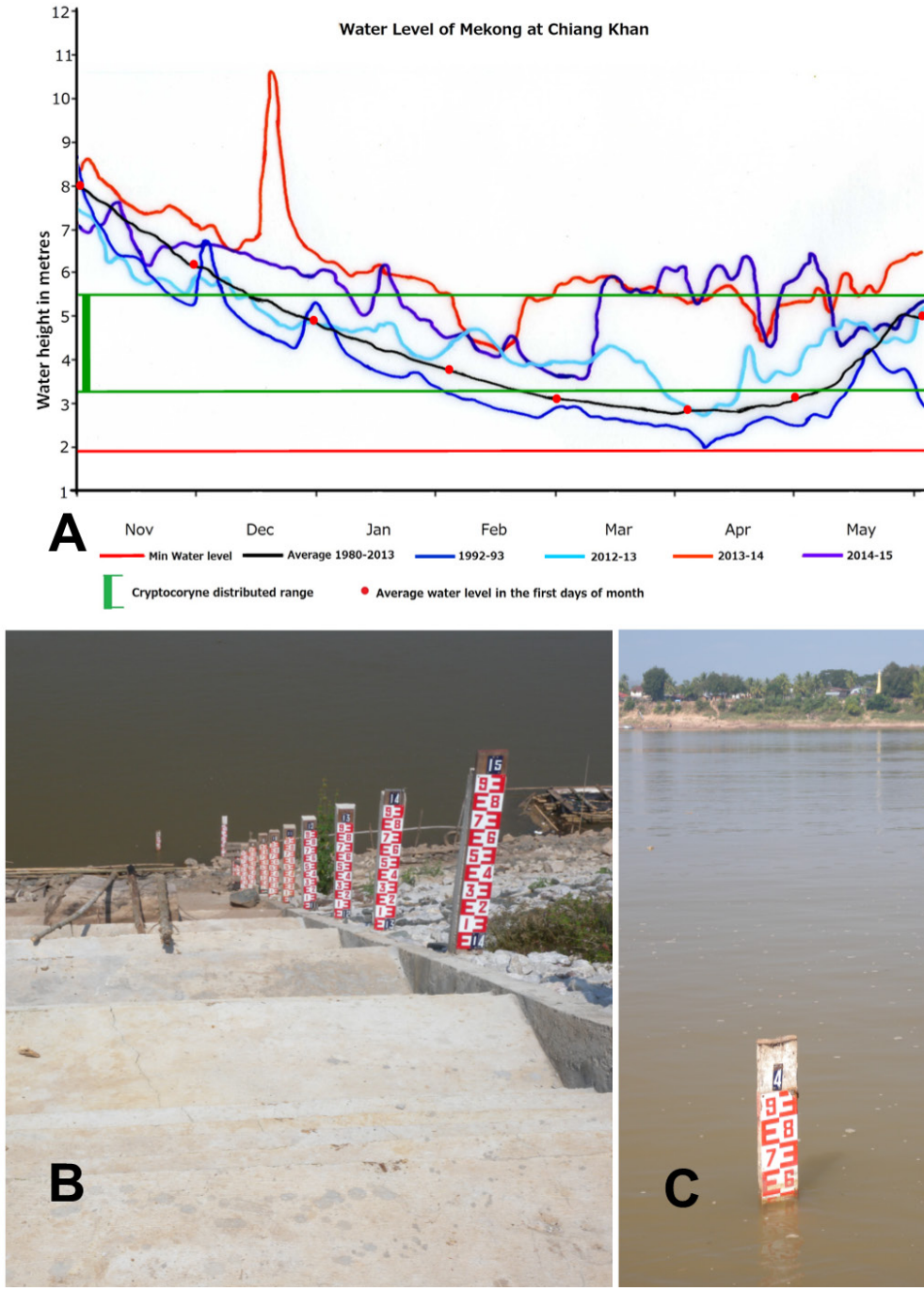

Figure 3. A. Water level at Chiang Khan for selected years. The average value is based on data from 1980 to 2013. Redrawn from the Mekong River Commission (2017); B. Water level scales by Chiang Khan on 1 January 2010 measured in relation to the zero gauge at Chiang Khan town (194 m above MSL); C. The water level of 3.6 m as shown in B.

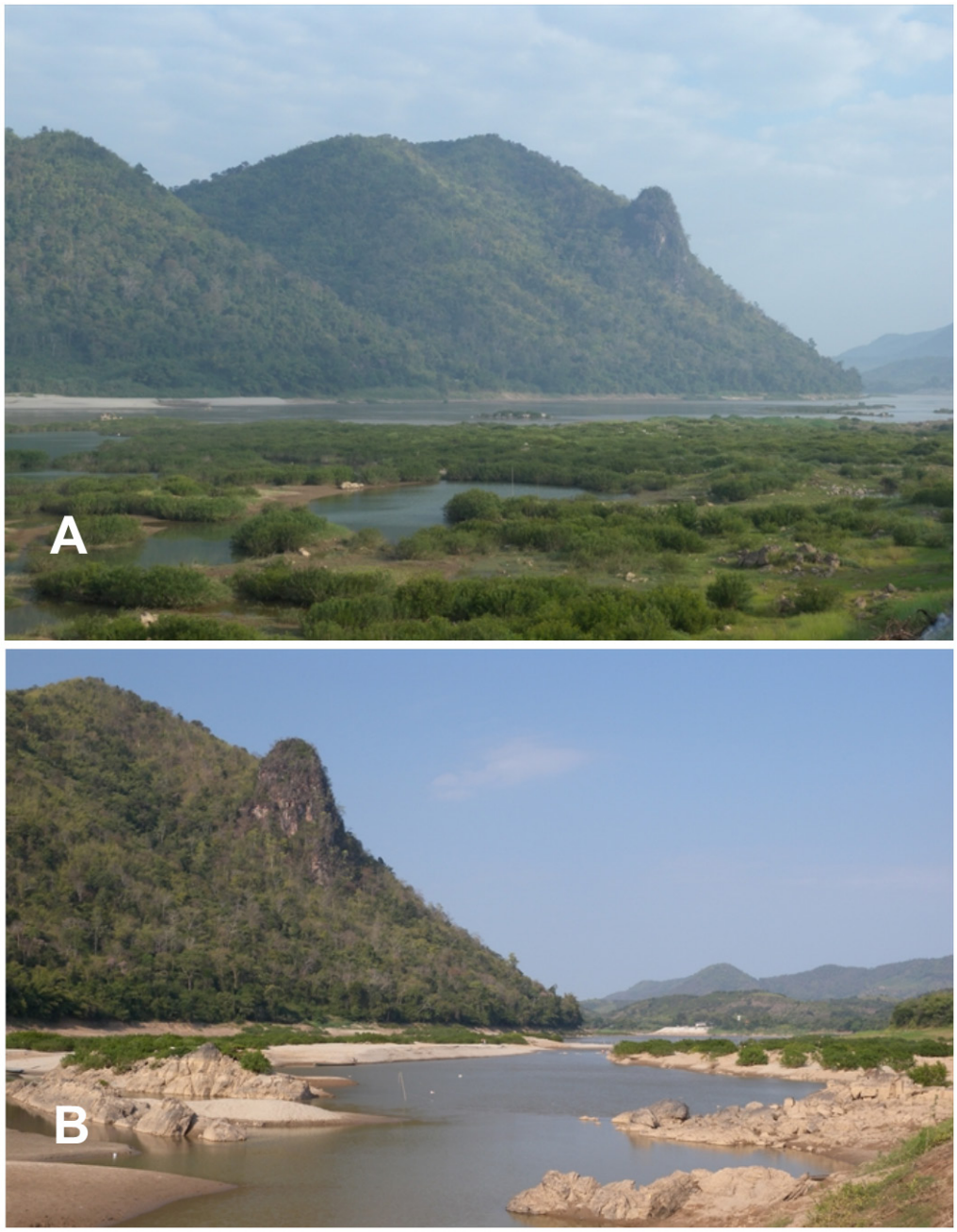

Figure 4. A. general view downstream at Ban Pah Baen, 21 January 2011, showing wetlands with creeks and stagnant pools among the shrubs; B. The edge of the flood plain near to the perennial channel looking downstream, 13 January 2010. Between the emerging rocks, sandbars and moving detritus accumulate.

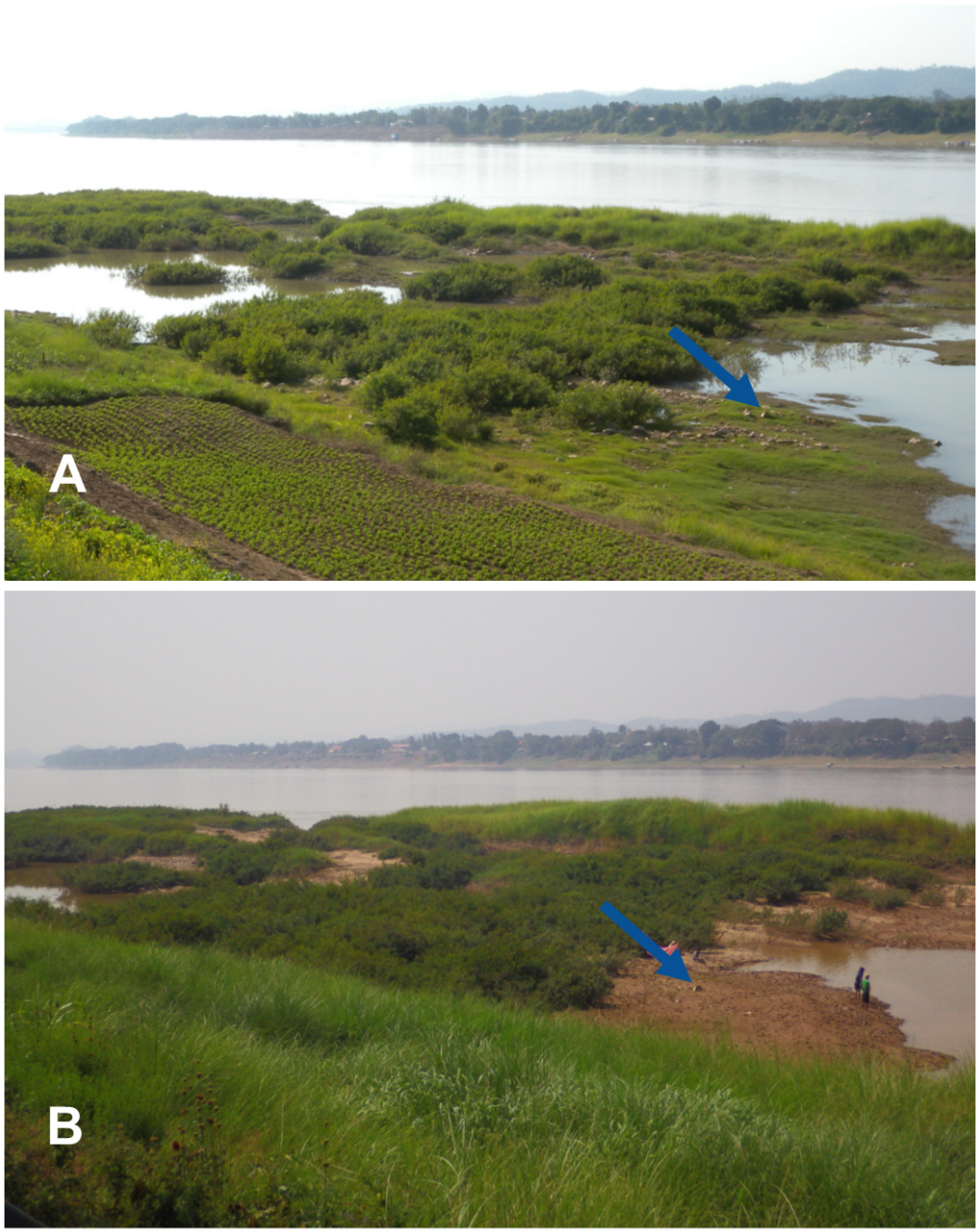

Figure 5. Change in the river bed structure at the eastern part of Chiang Khan: A. The river bed characterized by a green carpet on the low lying areas with many stones (arrow) and the water surface noticeable to the left, 21 January 2011; B. The same place as A, but the water has just receded, with mud flats left bare to the right and the stones visible in A can barely be seen on 15 February 2015.

Mekong vegetation between Kratie and Stung Treng, Cambodia. Scrub thicket is found in various places associated with *Cryptocoryne* habitats at Chiang Khan. The vertical distribution range of the rheophytes is wider than for *Cryptocoryne*.

CRYPTOCORYNE IN CHIANG KHAN

Cryptocoryne crispatula var. *crispatula* (short tube – including *C. crispatula* cf. var. *yunnanensis*) accounts for about 60% of the observed *Cryptocoryne* populations, *C. loeiensis* about 30%, while *C. crispatula* var. *crispatula* (long tube) amounts to about 10%. A minority of natural hybrid types were also observed. *Cryptocoryne loeiensis* coexists with *C. crispatula* var. *crispatula* (short tube) in many places. *Cryptocoryne crispatula* var. *crispatula* (short tube and long tube) are situated across the whole vertical distribution. *Cryptocoryne crispatula* var. *crispatula* (short tube) is found from above the 3.5 m water level to around a water level of 5.0 m. *Cryptocoryne crispatula* var. *crispatula* (long tube) is sparsely situated in the highest part around water level 5.5 m including the "slope part" adjoined to the riverbank, from about water level 4.0 m and may be found in large patches. The *C. crispatula* morph with the long, white spathe is only seen a few places between the immobile stones or sedimentary rock in the deepest part of the river. *Cryptocoryne loeiensis* is almost exclusively situated also with natural hybrid types in the 3.6 m to 4.0 m water level.

HABITAT

Bedrock bottom: Although the midstream and lower stream region of the Mekong comprises sandy riverbed, some bedrock sections are seen around Chiang Khan (Figs. 6 & 7). The bedrock zone is an important requirement for *Cryptocoryne* distribution in the Mekong as it is a stabilizing factor for the rheophyte shrubs and the retention of soil forming a suitable soil environment. The sedimentary rock of the places in which *Cryptocoryne* is found is rather brittle with conspicuous rock fissures and cracks. *Cryptocoryne* is found sheltered between relatively large stones, and the plants are not affected by the bottom flow during high water. Although the riverbed is firm owing to intermingled immobile stones in the sedimentary layer, surface accumulation and a certain amount of the substrate is constantly replaced by the undertow. The sedimentary rock, which is the basis for the establishment of the habitat, is full of fractures providing a good situation for the roots of rheophytes that develop in the cracks of the bedrock (Figs. 6 & 7). *Cryptocoryne* is a pioneer species here, with the majority of individuals found in open spaces or in gaps between the rheophytes.

Niches: *Cryptocoryne crispatula* var. *crispatula* (short and long tube), *C. loeiensis*, and the natural hybrids are usually seen as separate patches but may occur mixed. The *Cryptocoryne* are the inhabitants of the relatively open zone at the margin of the rheophytic scrub thicket or the vegetation-gaps, but do not inhabit the interior scrub thicket which is a shaded area covered by woodland canopy, nor between the roots of the scrub rheophytes that develop laterally and cover the substrate forming an impenetrable mesh.

Substrate: The substrate varies, but no difference in the habitat niche conditions has been observed. Total substrate accumulation above the upper part of the rhizome is generally up to 20 cm. The depth of the accumulated substrate layer varies from 10 cm in the usual habitat to a depth of more than 50 cm. The substrate pH is around 6.3–6.8.

Riverbed temperature: In April 2010 the air temperature of the habitat at 08.00 was 23–26°C in clear weather, and the surface temperature of the riverbed 25–27°C. In the same spot, the highest temperature in the daytime reaches 35–40°C under direct sunlight. The surface temperature of the heated bare riverbed rises up to 40–55°C. Temperature in the soil at a depth of 20 cm at the time was ca 28–35°C. Thus the difference of the vertical temperature frequently varies more than 20°C for the individual plants. Although such a high temperature is unusual in *Cryptocoryne* habitats in general, it occurs very often during the dry season in the Mekong.

LIFE CYCLE SUMMARY

Beginning growth: The *Cryptocoryne* of Chiang Khan are dormant with short, dark brown terete bristle like leaves during the high water period (Figs. 7C & 8). The vertical position of a habitat and its relation to a "seasonal water level decline" greatly influences the ecology and habit of the plants. The

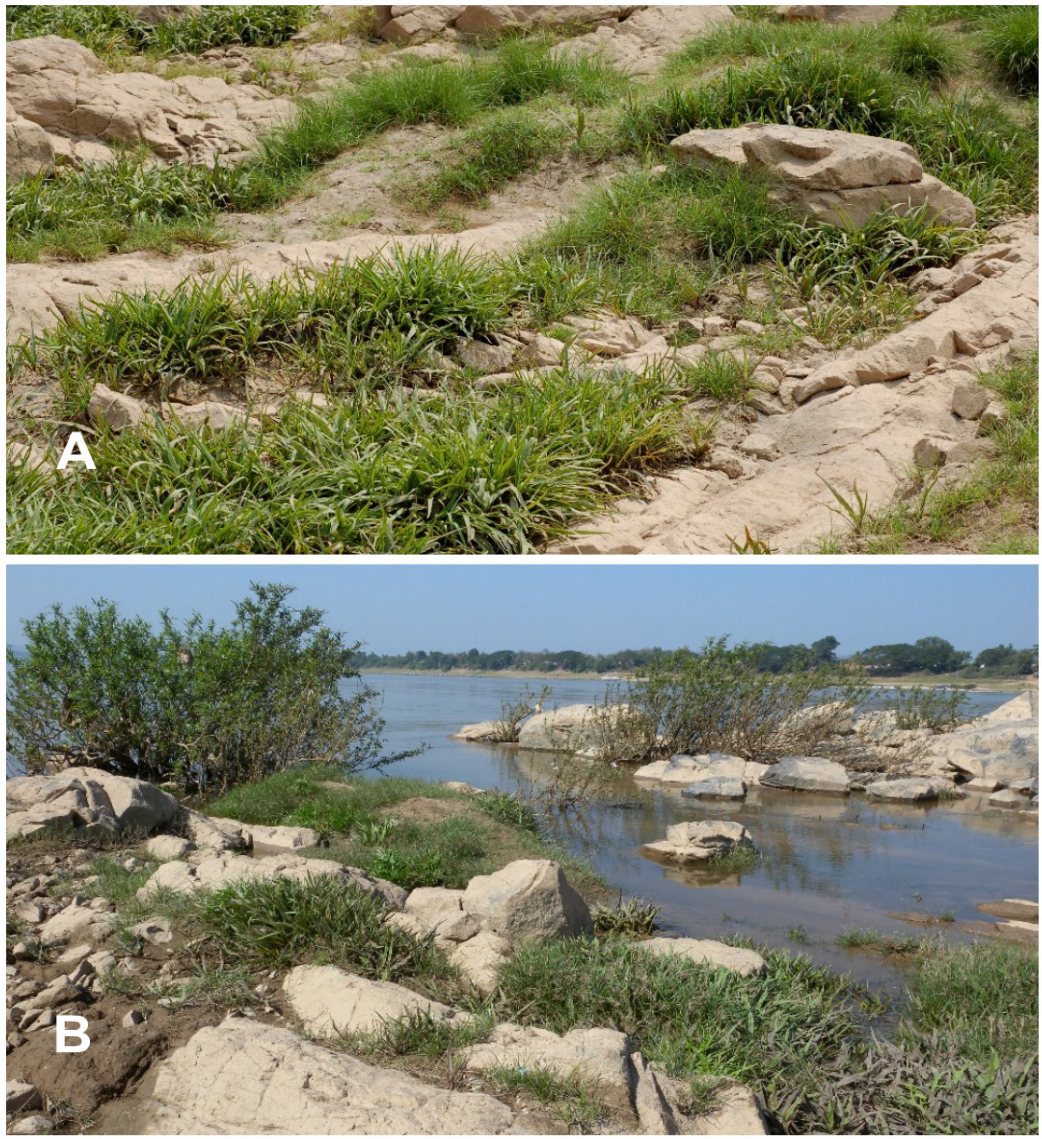

Figure 6. A. *Cryptocoryne* plants situated in cracks of the sedimentary rock in late growing season, with weeds, 17 March 2007, east of Chiang Khan; B. Patches of *Cryptocoryne* situated between the rocks near the edge of the flood plain, 18 January 2010, east of Chiang Khan.

shallow water level at each vertical position causes repeated submergence and emergence of plants owing to water level fluctuation over small time scales, e.g. hours and minutes as the mean level lowers over the course of the dry season. Under such a progression, the terete leaves are followed by narrow hard, reddish brown leaves that are undulated, with the new leaves producing larger and larger blades (Fig. 8B).

Noticeable plant activity starts when the water depth declines continuously and becomes shallower than 20 cm. Therefore, re-growth starts in early to mid-December when the water level is 5.5 m. Water level in mid-December is generally less than 5.5 m with swift, muddy streams still flowing over the floodplain.

Middle growth: The middle growth period occurs when the plants become completely emergent. The

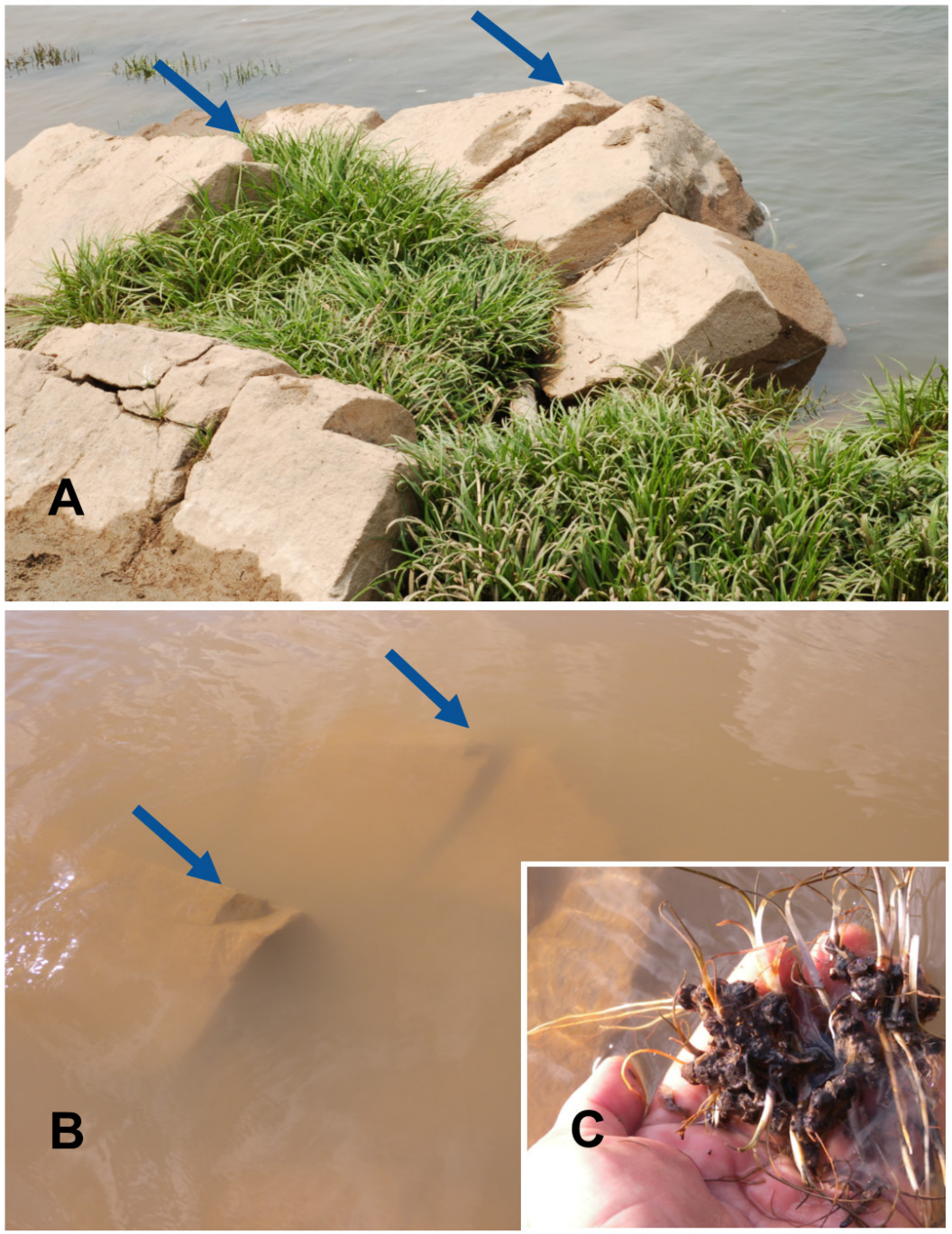

Figure 7. *Cryptocoryne* situated in cracks in the bedrock in the eastern part of Chiang Khan. A. An emergent situation with a luxuriant growth with plants tightly tucked into the cracks, 13 March 2007; B. The same situation as in A but in a submerged state, where some characteristic rock features (arrows) can be seen, 10 January 2010; C. Excavated *Cryptocoryne* rhizomes with narrow terete leaf blades of the submerged plants from B (as seen in A) showing the characteristic modules.

Figure 8. A. *Cryptocoryne* beginning to grow in shallow water, with terete leaves followed by narrow, stiff, reddish brown leaves with an undulating margin; Chiang Khan eastern part, 11 January 2010; B. *Cryptocoryne* already emergent, at the start of the middle growth season, leaf blades are still rather stiff, reddish brown with an undulating margin; Chiang Khan eastern part, 11 January 2010.

transition period to the long narrow green or brown leaves that are typical adult leaves requires more than three weeks of growth. Simultaneously, as growth continues, the markedly undulating margin gradually disappears, and the leaf blade width increases (Fig. 8B). Each patch has various leaf colours, from dark-brown to green, depending on the exact location or habitat of the plants. The maximum active leaf number of individual plants is ca 25.

End growth: The habitat is in its driest and warmest state during the middle of March to the middle of April just before the rainy season starts (Fig. 9). All the patches are emergent, and most *Cryptocoryne* are developing new leaves. The moisture of the surface soil varies with the stone or rock arrangement, vicinity of rheophytes, etc. When the dry state further progresses, the dead *Cryptocoryne* leaves remain in patches.

Dormancy: Water level begins to rise after the middle of April with the muddy water usually containing many soil particles. From June, all *Cryptocoryne* patches are under water. When the leaves become submerged they begin to melt and disintegrate, and *Cryptocoryne* will soon become dormant. Each plant develops less than ten dark brown terete leaves with a length less than 3 cm, and a width less than 2 mm. This occurs during the highest hydraulic pressure situations in all the *Cryptocoryne* habitats during the rainy seasons.

Supplementary notes: The Mekong has, in recent years, changed from a situation of natural water level fluctuations arising from seasonal precipitation to artificial water level fluctuations due to up-stream dam operations. This results in long-term drying or long-term submergence according to riverbed level. In addition, the water level can suddenly rise by up to 1 m in a day, and if that water level continues, the riverbed emergent period necessary for normal *Cryptocoryne* growth is obstructed.

The start date of re-growth is variable, corresponding to the water level, which varies from year to year (Fig. 3). In a period of growth with a water level below 4 m, the longest period can be more than four months from the beginning of January to the middle of May in dry year, as in 1992. However, 2014, which was an exceptional high water situation, *Cryptocoryne* were completely inactive due to constant high water level. In 2015, patches that were already in the transition stage to an emergent condition in February, had only sparse re-growth owing to a surface accumulation of more than 20 cm of mobile detritus. Then, water level below 4 m lasted for only 17 days (21 February–9 March); the large majority of plants had not undergone their usual growth activity for two years.

The spathe: During the flowering period from the middle to end of December to the middle of February, up to four simultaneously open spathes on one plant have been observed. Flowering becomes possible when the water level becomes lower than the riverbed surface and the flowering period is less than three weeks duration. The opening period of a spathe is three days and pollination is performed by various small fly species. The kettle part of the spathe is situated deep in the riverbed, and the syncarp matures in that position. Although the upper part of immature, exposed syncarps have been seen above the riverbed soil in several instances, opened syncarps have not observed. If the pattern is similar to that of *C. crispatula* from Peninsular Thailand, syncarps would mature about a year later at a time of low water, and later in the year than the observation period of the present study.

Rhizome and root system: The rhizome is usually situated deeper than 10 cm in the substrate, with several contractile roots further anchoring them deeply and helping stabilize them under unstable situations in a riverbed with a swift bottom flow during high water. Several upright, finely branching roots reaching above the soil surface may form a carpet-like growth. The creeping rhizome (Fig. 10 & 7C) shows an activity period during the dry season and a dormancy period during the rainy season, i.e., the swelling and constriction of one section, one "module" (Hallé & Oldeman, 1970, or one "article" sensu Engler, 1877). Rhizomes with up to ten years of modules have been observed in *C. loeiensis* and *C. crispatula* var. *crispatula* – long tubed spathe, which resemble pearls on a string. Subterranean stolon propagation is usually seen and may enter into a patch of a different species or variety that is close by. A lateral sprout of the rhizome, thereby forming "rhizome agglomeration", often occurs. The quantity of agglomerations and stolons show the minimum semi-stable period of the riverbed at each place. The rhizome of *C. loeiensis* has been found

Figure 9. A. Stagnant pools with clear water at the peak of the dry season near Ban Hat Bia, 1 April 2006; B. River bank west of Kaeng Kood Koo towards the end of the growing season for plants situated near water level 5 m, 15 March 2010. Weeds are prominent on higher ground at this time.

Figure10. Excavated *Cryptocoryne crispatula* var. *crispatula* rhizome of more than eight years of age showing the characteristic enlarged modules of the rhizome. Chiang Khan, January 2010.

with a diameter up to 1.5 cm, and a total length of more than 10 cm. The rhizome of *C. crispatula* var. *crispatula* has been found with a diameter up to 2.2 cm, and a length longer than 14 cm. The maximum length of contractile roots is over 50 cm.

TAXONOMY

The taxonomy of the species of *Cryptocoryne* has been dealt with in the volume of the 'Flora of Thailand': Araceae (Jacobsen *et al.*, 2012), so this will not be dealt with here in detail, but some of the characteristics are below described.

Cryptocoryne crispatula Engl. var. *crispatula* – long spathe tube (Fig. 11A).

This species is based on material from the Mekong at Se Lam Phao; the type specimen is a plant with a long tube to the spathe (*Harmand 65*, holotype **P!**, isotypes **B!**, **BM!**, **K!**, **P!**).

Leaves 10–30 cm long, blade linear to lanceolate 0.5–1.5 cm wide, green to brownish (markings in open sun), smooth to undulate at margin; margin mostly entire, blades usually more or less upright, often rather stiff (lax in shaded places). Spathe 10–25 cm long, limb slender, 2–8 cm long, more or less spirally twisted, yellowish to greyish to greenish, with short to long, usually purple (sometimes black purple) markings (sometimes almost completely covering the inner surface or completely missing).

Cryptocoryne crispatula Engl. var. *crispatula* – long spathe tube – entirely white (Fig. 11B).

Leaves 20–30 cm long, blade 0.2–0.4 cm wide, flaccid, green to brownish, smooth to somewhat denticulate at the margin. Spathe 12–20 cm long, limb slender, 2–4 cm long, spirally twisted and entirely white, sometimes slightly purple on the outside. The spathe has a distinct sweet honey-like smell (most *Cryptocoryne* species smell like a rotting meat).

Plants with a similar appearance but with browner leaves and spathe which is purplish have also been found, and it is unknown if this plant is more related to the plant with the white spathe or the "normal" var. *crispatula*.

Cryptocoryne crispatula Engl. var. *crispatula* – short spathe tube (Fig. 12A, C, H).

Leaves 10–30 cm long, blade linear to lanceolate, 0.5–1.5(–2.5) cm wide, green to brownish to red brownish (markings in open sun), smooth to undulate at the margin, margin entire to finely or distinctly irregularly denticulate, usually upright to

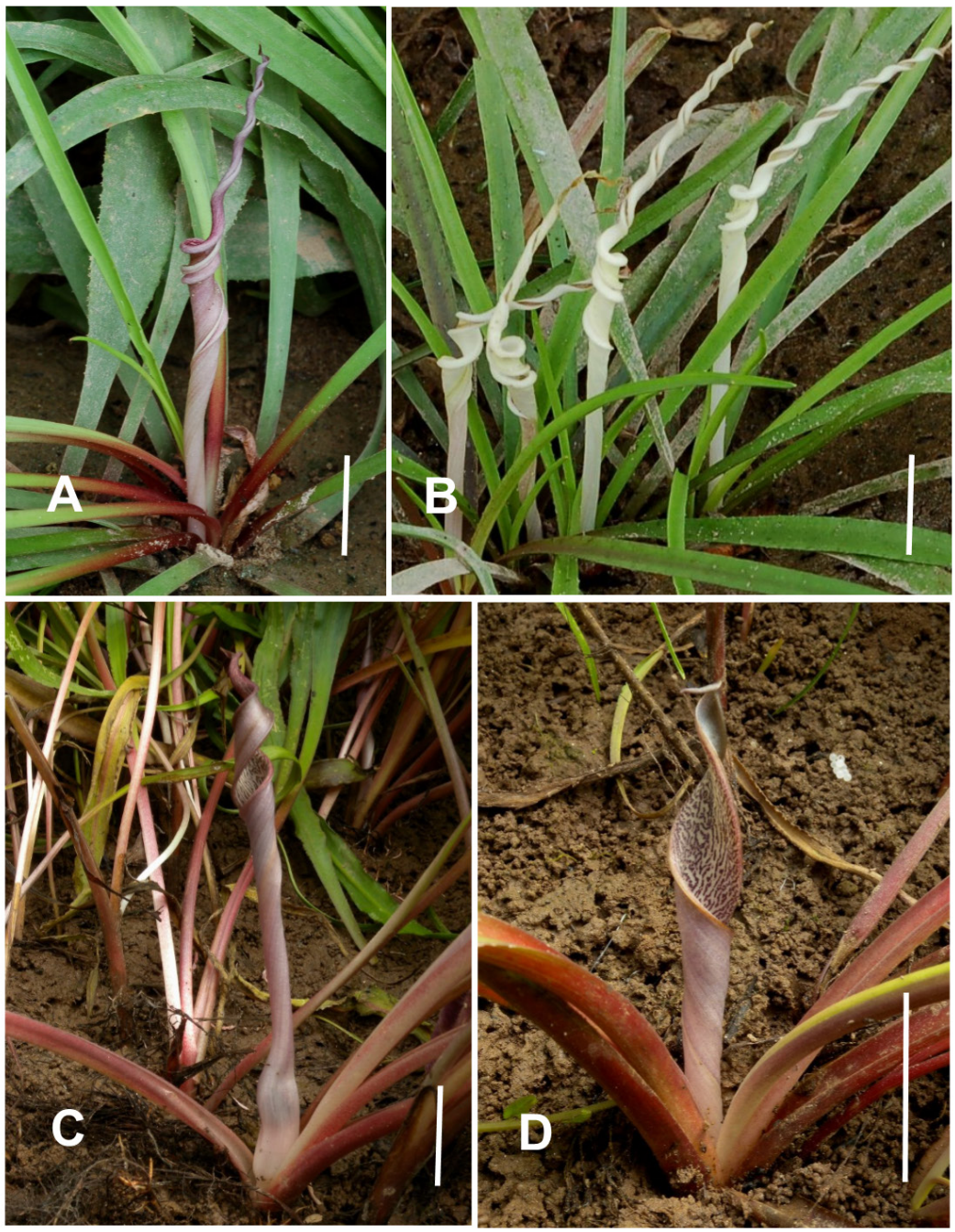

Figure 11. *Cryptocoryne* spathes from the Chiang Khan region. A. Typical *C. crispatula* var. *crispatula* with a long tube and a spirally coiled spathe limb (Chiang Khan eastern part, 15 March 2007); B. *C. crispatula* var. *crispatula* with a long tube and an entirely white and spirally coiled spathe limb (Chiang Khan western part, 14 March 2007); C. *C. crispatula* var. *crispatula* hybrid with a somewhat short tube and a rather short spathe limb (Ban Pah Baen, 17 January 2010); D. *C. crispatula* var. *crispatula* hybrid, with a short tube and a rather short, and open spathe limb (Ban Pah Baen, 17 January 2010). Scale 2 cm.

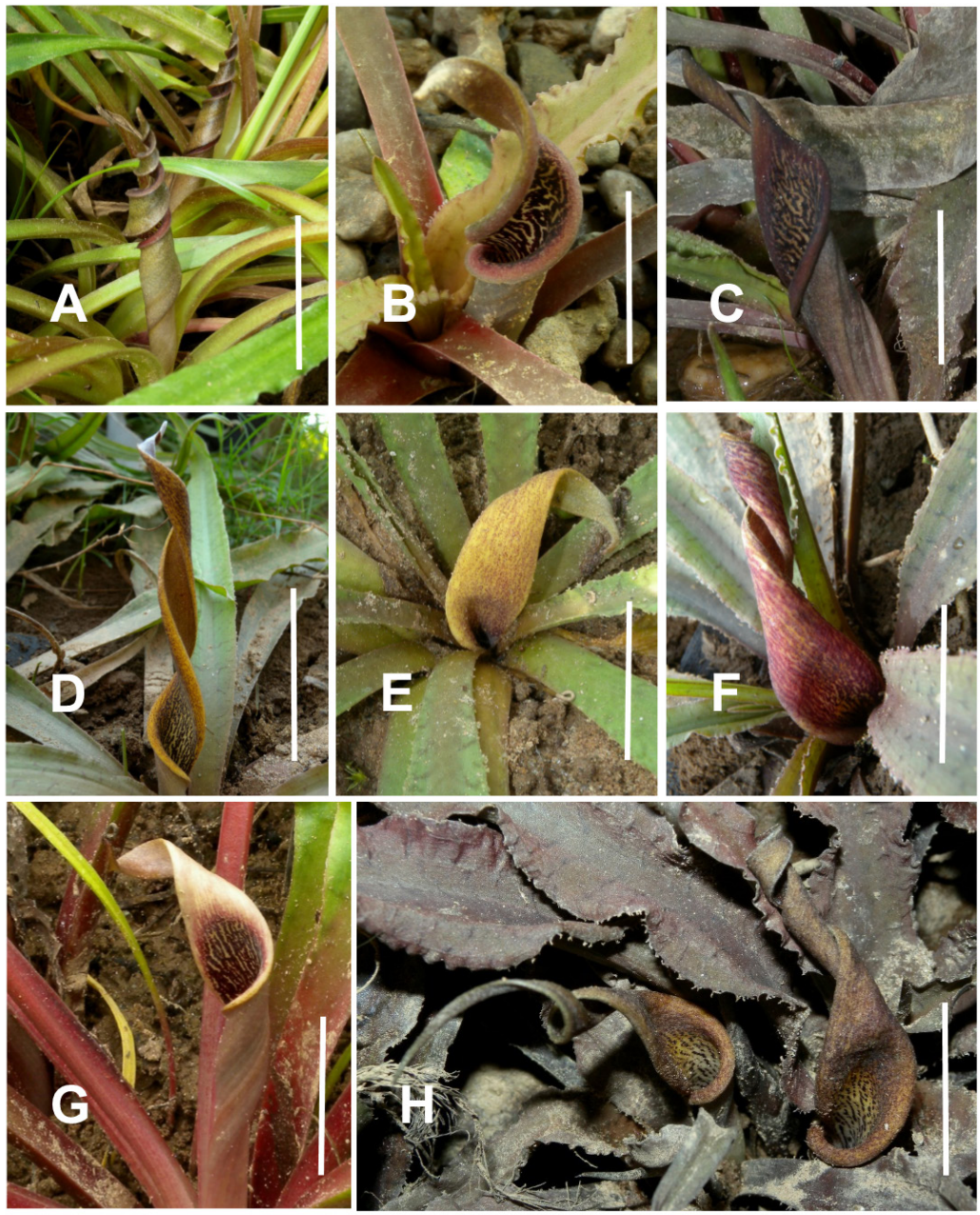

Figure 12. *Cryptocoryne* spathes sampled from the Chiang Khan region, with short tubes and varying degrees of coiling and colouring of the spathe limb, indicating a hybrid origin. A. *C. crispatula* var. *crispatula*, short tube, with a just-opening spathe limb still showing a rather long spiral (Chiang Khan eastern part, 17 January 2010); B. *C. crispatula* cf. var. *yunnanensis*, short tube, a spathe with a short spiral with black-purple markings on the inner surface (Chiang Khan eastern part, 17 January 2010); C. *C. crispatula* var. *crispatula*, short tube, with dark markings on the inner surface of a backwards-bent spathe limb (Chiang Khan eastern part, 18 January 2010); D. Hybrid with a short tube, a long, somewhat spirally coiled, yellowish spathe limb with few markings on the inner surface (Chiang Khan eastern part, 21 January 2011); E. Hybrid with a yellowish, recurved spathe limb with spotted dense patterning (Chiang Khan eastern part, 15 January 2010); F. Hybrid with a reddish, recurved spathe limb with elongate dense patterning (Chiang Khan eastern part, 21 January 2011); G. Hybrid with markings in the tube opening, but spathe limb recurved with the markings fading distally (Ban Pah Baen, 17 January 2010); H. Brownish, recurved spathe limb with a dense colour on inner surface and spotting in the tube opening; note also the irregular denticulations of the leaf margins (Chiang Khan eastern part, 10 January 2010). Scale 2 cm.

flat on the soil, rather stiff. Spathe robust, 6–12(–14) cm long, limb robust, 2–4 cm long, shortly spirally twisted, greyish with short to long, usually distinct strong black-purple markings of various shapes, sizes and intensities, sometimes almost wholly black-purple.

Cryptocoryne crispatula Engl. cf. var. *yunnanensis* (H.Li) H.Li & N.Jacobsen (Fig. 12B).

Leaves 10–30 cm long, blade 0.5–1.5 cm wide, usually, green to brownish with markings, smooth to somewhat undulate, margin entire to finely or distinctly irregularly denticulate, spathe with a rather short tube, 8–12 cm long, limb with a rather short, thick spiral with a yellowish base colour and purple-reddish spots.

The plants from Chiang Khan referred to var. *yunnanensis* differ a little from the plants from the more northern sites at Chiang Khong and in Yunnan (Li & Jacobsen, 2010), and the Lao P.D.R. by having a darker spathe and spots, and the margins of the spathe are darker. Plants are not numerous at Chiang Khan. It could be that the Chiang Khan plants referred to var. *yunnanensis* also belong to the extensive hybrid complex discussed below.

Cryptocoryne crispatula Engl. – deviating plants or hybrids?

There are a number of plants at Chiang Khan that deviate from the ones mentioned above in spathe morphology. All have rather short spathes of about 10 cm in length. The leaf blades of these plants fall within what is known from the populations in general: green in shaded positions, brownish to dark brown in open positions, and blades with an undulate margin, which often has distinct irregular denticulations especially in sun-exposed situations.

Different types of spathe limbs may be characterized as follows:

a. Short, upright, coiled or open spathe limb with spots and lines (Fig. 11C–D).

b. Narrow yellow upright limb without any markings on the inner surface (Fig. 13A).

c. Broad yellow recurved limb with or without markings on the inner surface (Fig. 12E).

d. Yellowish upright or recurved limb with stripes or markings on the inner surface (Figs. 12D; 13B).

e. Brownish upright to recurved limb with a more or less brown inner surface (Fig. 12C & H).

f. Brownish to almost reddish somewhat rough inner limb surface (Fig. 12F).

g. Markings in the tube opening but fading distally on the recurved limb (Fig. 12G).

A common feature for almost all of these types is that the inner surface if the spathe tube below the limb is spotted or striped reddish to purplish. The above-mentioned types are not discrete entities, with almost all intermediate forms to be found.

Although a recurved spathe limb not seen so often in *C. crispatula*, there are reports from Lao P.D.R. where forms regarded as belonging to *C. crispatula* s.l. have a yellowish-whitish, spotted recurved limb of the spathe: Tam Leuk (Linke, 1997; as *C. albida* Parker) and Nam Chim (as var. *crispatula*), as well as var. *yunnanensis* (as var. *sinensis* (Merr.) N. Jacobsen) has been found at Nam Lik (Andersen *et al.*, 2006).

Molecular analysis of plants similar to these from Tam Leuk, Lao P.D.R. resembling *C. albida*, have been shown to fall outside the *C. albida* types from southern peninsular Thailand and Myanmar, but are more related to northern Thai and Lao populations of *C. crispatula* (Jacobsen *et al.*, 2015).

Cryptocoryne loeiensis Bastmeijer *et al.* (Fig. 14A–D).

This species is based on material from Chiang Khan and has until now only been found there (Bastmeijer *et al.*, 2010; *Bastmeijer 1145a*, holotype **BKF!**; isotypes **C!**, **L!**).

The leaves resemble some of the forms of *C. crispatula* found in the area: Leaves up to 30 cm long, blade to 1.5 cm wide, margin somewhat undulate, irregularly denticulate, green to brownish and with brownish markings. Spathe ca 4–6 cm long, limb evenly purple to brown to black brown purple, obliquely forward twisted, with inner surface evenly rough throughout, and lacking a collar.

There are also plants which have a brownish, open spathe limb like *C. loeiensis* but with markings in the throat of the tube resembling those found in *C. crispatula*. These may be hybrids (Fig. 14E–F).

Figure 13. Plants of *Cryptocoryne* sampled from the Chiang Khan region, with short tubes and a rather open yellow spathe limb, indicating that they are of hybrid origin. A. Showing an all yellow upright spathe limb (Chiang Khan eastern part, 11 January 2010); B. Showing a slightly twisted spathe limb with purplish shading towards the tube opening; notice the irregular denticulations on the leaf blade margins (Chiang Khan eastern part, 15 January 2010). Scale 2 cm.

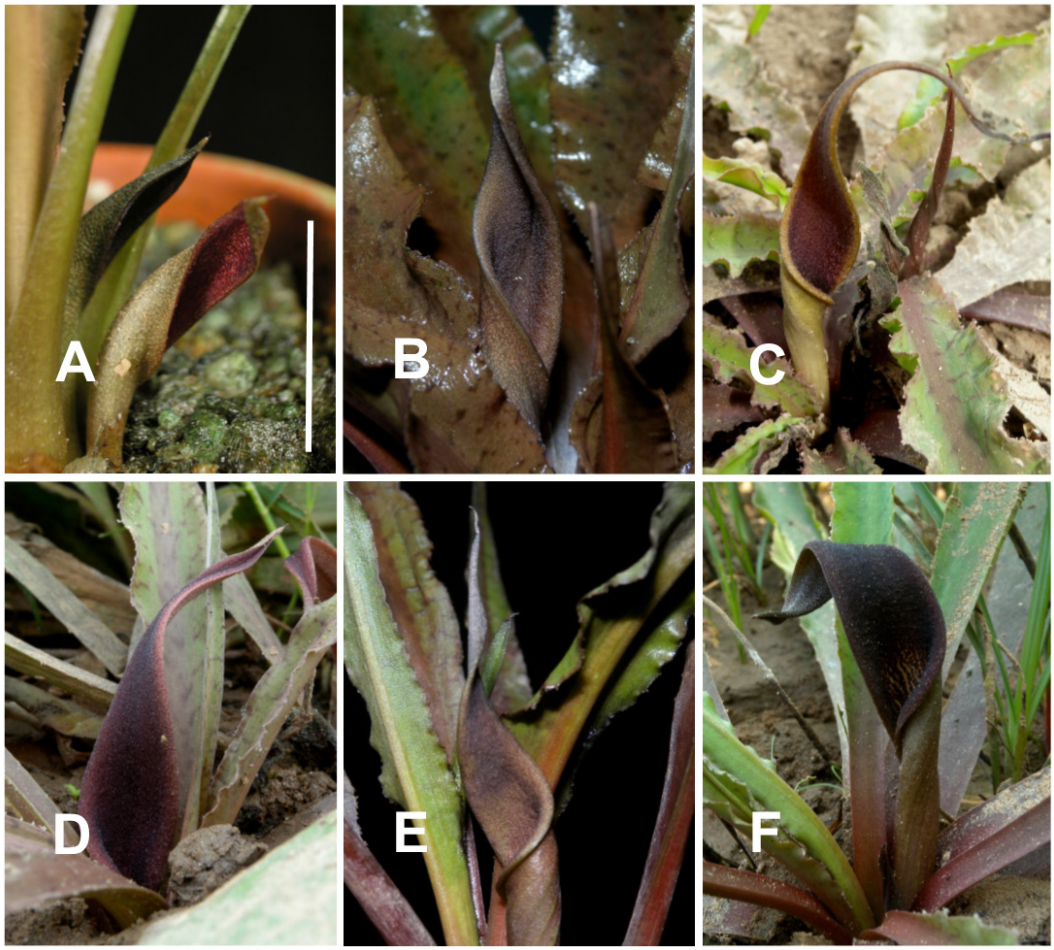

Figure 14. *Cryptocoryne* plants from Chiang Khan Region. A. *C. loeiensis*, type specimen, cultivated, *Bastmeijer 1145a*, showing the short, obliquely twisted spathe limb; note the colour difference on the inner surface of the spathe limb in the oldest and youngest spathe; B. *C. loeiensis*, showing a more upright spathe limb (Chiang Khan eastern part, 10 January 2010); C–D. *C. loeiensis*, sampled from Chiang Khan, showing a little different shape and colouring of the spathe limb (Chiang Khan eastern part, 21 January 2011; E–F. Assumed to be *C. loeiensis – C. crispatula* hybrids from Chiang Khan with a relatively longer tube and markings in the spathe tube (Chiang Khan eastern part, 21 January 2011). Scale 2 cm. Photo A by J.D. Bastmeijer.

DISCUSSION

The number of *Cryptocoryne* at Chiang Khan is overwhelming. From this and other studies (Li & Jacobsen, 2010; Idei *et al.*, 2010; Jacobsen *et al.*, 2012) it can be concluded that *Cryptocoryne* are a prominent element in the Mekong, both in the main course and probably in most of the Mekong catchments area, not least in its tributaries. An observer must be there at the time of flowering, as the narrow grass-like leaves may not be recognized, or they may be totally dried out. From the documented material available (Jacobsen *et al.*, 2012 & 2016, and unpublished) it is also likely that *Cryptocoryne* also occurs in the rivers and streams in the adjacent regions.

From the studied areas around Chiang Khan, it is obvious that *Cryptocoryne* does not occur as continuous carpets along the Mekong, but in more or less scattered places along the main river course.

Puff & Chayamarit (2011) did not record *Cryptocoryne* in the Pha Taem N.P. area, but this could be owing to the difficulty in finding them:

Cryptocoryne mekongensis has been found on two adjacent islands just at the Mekong–Mun River confluence as well as a little upstream in the Mekong. *Cryptocoryne mekongensis* was described from Don Khon, Champasak Province, Lao P.D.R, and has also been found in Kratie Province in Cambodia and Khong Chiam District in Thailand (Idei *et al.*, 2010; Jacobsen *et al.*, 2012).

The *Cryptocoryne crispatula* complex and other narrow-leaved Thai *Cryptocoryne* seem to be found in areas with limestone components rather than regions with a highly acid bedrock, such as granite. These soils are naturally mixed in many rivers and streams, but usually resulting in not very acidic soil and water conditions.

From our experiences in Thailand we would say that the *C. crispatula* types with long tubed spathes are found in habitats where there is or may be some water at the time of flowering, i.e., with a higher or maybe fluctuating higher water level during flowering, while the short tubed types are found along larger rivers or streams with a great water seasonal fluctuation and a water bearing that is always low during the dry season, such as the Mekong, where the success of flowering depends on complete emergence. We interpret the presence of long tubed *C. crispatula* at Chiang Khan as plants or seeds that have been washed downstream from smaller tributaries into the Mekong and have landed in suitable places where they are able to reproduce and perhaps also hybridize with other flower types present (Jacobsen *et al.*, 2015 & 2016).

Many *Cryptocoryne* have a proliferous mode of vegetative propagation via long subterranean stolons, which may easily attain a length of 20–30 cm. In a number of instances as seen in Chiang Khan, not all plants show this vegetative propagation. It may be that mature plants under stable growth conditions do not produce many stolons but rely on production of new modules on their rhizome each year. Nevertheless, under more unstable conditions, such as newly established habitats, stolons tend to proliferate.

Apparently much introgression can be found between the different forms; the situation at Chiang Khan – and the Mekong and tributaries – deserves a much more thorough investigation.

THE FUTURE

Cryptocoryne habitats in the Mekong may be threatened. The ecological niches are dependent on natural seasonal water level fluctuations. Dam construction created a large upstream water reservoir over *Cryptocoryne* habitats. As of 2017 six major hydroelectric dams are already operating in Yunnan Province, China, in the northern part of the Mekong. A further 14 more dams are under construction or being planned in Yunnan and Tibet.

In addition a total of 11 dam projects are advancing in the Mekong midstream region and lower stream region. About 55% of this river course will be dam reservoirs, almost all bedrock sections which *Cryptocoryne* inhabit will be submerged by the reservoirs. In the future, the whole habitat area described here will be completely submerged on the "step" between these two dams. This may mean the extinction of *C. loeiensis* together with other *Cryptocoryne* in the area.

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