A rare endemic Thai yam rediscovered: *Dioscorea inopinata* Prain & Burkill (Dioscoreaceae) and its affinities

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ABSTRACT. Dioscorea inopinata Prain & Burkill was collected at Khao Sam Roi Yot National Park in 2002 for the first time in over 70 years. The specimens included female plants. This species was formerly known only from males. This allowed a full description and illustration of the species to be produced. The new morphological data are used to re-assess the plant's relationships and origins. It appears to be a member of Dioscorea sect. Enantiophyllum Uline with atypical wholly alternate leaves and obtuse to acuminate, more or less lanceolate tepals. It is endemic to Khao Sam Roi Yot and thus a candidate for autecological and conservation studies.

INTRODUCTION

When work to prepare a treatment of Dioscoreaceae for the Flora of Thailand began in 1996, *Dioscorea inopinata* Prain & Burkill was known from just three specimens, all from Prachuap Khiri Khan Province, and all male plants. It was first collected by Kerr in July 1924 (*Kerr* 10978), whose specimen was the basis for its description by Prain & Burkill (1927). In their account of Asian *Dioscorea* (Prain & Burkill, 1938) they were able to cite two further specimens, a collection made by Kerr in July 1931 (*Kerr* 20512) and one made by Lakshnakara which has not been located in any of the herbaria used in this study (see Materials and Methods). It was therefore imperative to look for this species to discover if it was still extant 70 years after it was last collected, and to complete its description by finding female flowers and fruits. It was collected by two groups of researchers in 2002. David Middleton and Somran Suddee found male plants at Khao Sam Roi Yot in August, and the authors found female plants in the same area in early December. This allowed a complete description and illustrations to be provided below.

In addition to having a very restricted distribution, *D. inopinata* was singled out by Prain & Burkill (1936) as a species with an unusual combination of morphological characters. Its stem twines to the right (dextrorse in the sense of Burkill, 1960). In the old world tropics, all such species have been placed in *Dioscorea* sect. *Enantiophyllum* Uline. It is also wholly glabrous, as are most species of that section. The leaves of *D. inopinata* are alternate, however, while in the species of *D.* sect. *Enantiophyllum* they are usually opposite. Its tepals are elliptic-oblong, with acute or acuminate apices in the outer whorl,

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unlike the typical ovate to orbicular tepals with rounded or obtuse apices of the right-twining section. These characters, in particular the tepal shape, led Prain & Burkill (1936) to suggest that *D. inopinata* was related to the left-twining *D. bulbifera* L. and thus a member of *D.* sect. *Opsophyton* Uline. It is the only right-twining species not in *D.* sect. *Enantiophyllum* in the classifications of Prain & Burkill (1936, 1938) and Burkill (1960). They also hypothesised that the combination of characters found in the species was evidence of a hybrid origin, with the parents being a species of *D.* sect. *Enantiophyllum* and *D. bulbifera*. The new character data available allow this hypothesis and the relationships of this enigmatic species to be re-evaluated.

MATERIALS AND METHODS

The study of Dioscoreaceae for the Flora of Thailand treatment used 1220 specimens from Thailand at the following herbaria or on loan: AAU, B, BK, BKF, BM, CMU, E, K, L, P, Biology Department, Naresuan University, Phitsanulok (abbreviated as PNU in this paper), QSBG, and TCD. Abbreviations follow Holmgren & Holmgren (1990). Comparative morphology was used to delimit species in all cases.

DESCRIPTION

Dioscorea inopinata Prain & Burkill, Kew Bull. 245. 1927; Prain & Burk. in Ann. Roy. Bot. Gard. (Calcutta) 14(1): 134.1936. Type: Thailand, Prachuap Khiri Khan (Prachuap), Sam Roi Yot (Sam Roi Yawt), on rocky limestone hill, ♂ fl. 13 July 1926, *Kerr* 10978 (holotype K!; isotypes BK!, BM!). Fig. 1.

Slender climber to 4 m. Underground parts unknown. Indumentum absent. Stem 1.25-3 mm in diam. towards base, twining to the right, annual, unarmed, terete with shallow longitudinal ridges, usually wine-red in colour, sometimes green with scattered red-brownish blotches. Leaves simple, alternate, blades (2.2-)3-7 by (0.8-)1-3.5 cm, ovate to narrowly ovate, base cordate, sinus 0.1-4 mm deep, apices 1.5-6 mm long, acute to acuminate, margins entire; 5-7-nerved, only main vein and first vein pair reaching apex; chartaceous, green to dark green and glossy above, paler below; forerunner tips 1.5–3 mm long, brown to dark brown; petioles 5–10 mm long, shallowly angled, channelled above, colour as stem, lateral nodal flanges/spines absent. Cataphylls (Fig. 1B) 2-3.5 by 3-3.6 mm, ovate, apex obtuse, chartaceous, pale brown to brown. Bulbils absent. Inflorescences spicate, axes slender, angled, colour as stem; all bracts chartaceous, tepals inserted on a small discoid torus, erect, free, fleshy in texture with inner whorl tepal slightly thicker than outer, green-yellow. Male inflorescences (Fig. 1A, 1C) simple or compound (Middleton et al. 1181 only), compound inflorescences 2– 3.5 cm long, 1(-2) per axil, primary bracts (Fig. 1D, at inflorescence bases) 1.3–1.5 by 0.5–0.6 mm, elliptic-oblong, apices 0.2–0.4 mm long, acuminate; simple/partial inflorescences 1–2 per axil, peduncles 0.8–1.2 mm long, axes 0.7–2.6 cm long. Flowers ± patent to axes; floral bracts (Fig. 1F) 0.6–0.8 by 0.6–0.9 mm, ovate, apices 0.1–0.2 mm long, acuminate; bracteoles (Fig. 1G) 0.5-0.9 by 0.3-0.6 mm, ovate, apices 0.1-0.15 mm long, acuminate; outer tepals (Fig. 1H) 1.5-1.9 by 0.6-1.1 mm, ovatelanceolate to narrowly so, apex acute; inner tepals (Fig. 1I) 1.4-1.8 by 0.4-0.5 mm, narrowly elliptic to elliptic-oblong or lanceolate, apex acute to obtuse; stamens 6 (Fig. 1E),

inserted on torus, filaments 0.3-0.6 mm long, anthers 0.2-0.4 by 0.2-0.3 mm; pistillodes (Fig. 1E) 0.15-0.2 by 0.2-0.25 mm, erect, 3-lobed. Female inflorescences not seen. Old female flowers (Thapyai & Wilkin 513) with floral bracts (Fig. 1L) 1.4-1.5 by 1.1 mm, broadly ovate, apices 0.1–0.2 mm long, acuminate; bracteoles (Fig. 1M) 1-1.2 by 0.6-0.7 mm, ovate-lancelote, apices 0.1-0.3 mm long, acuminate; outer tepals (Fig. 1N) 1.5–2 by 0.8–1.1 mm, ovate, apices to 0.14 mm long, acute to acuminate; inner tepals (Fig. 10) 1.4-1.8 by 0.4-0.7 mm, elliptic to narrowly so, apex obtuse; ovaries (Fig. 1J) 3-5.3 by 0.9-2.3 mm, elliptic in outline, with 3 longitudinal ridges, green to dark green, glossy; staminodes 6 (Fig. 1K), 0.15-0.45 mm long, staminiform, inserted on torus; styles (Fig. 1K) 0.3-0.8 by 0.5-0.7 mm, fused for most of their length, erect; stigmas (Fig. 1K) 0.3–0.6 mm long, recurved. *Infructescences* (Fig. 1P) 6– 8 cm long; capsules (Fig. 1Q) 1.8-2.1 by 2.5-3 mm, broadly obovate in outline, base truncate, apices retuse, 0.7-1.4 mm deep sinus, capsular stipes 3-4 by 2-3.5 mm, obconic; immature capsules pale green to dark green and glossy, darker along axis and margins, sometimes with purple streaking or blotching; mature capsules deflexed at angle of 25°-45° to axis. Seeds (Fig. 1R) 3.5-5.3 by 4.5-6 mm, ovoid-lenticular; wings 14-15.5 by 13-14 mm, extending all around seed margin, broadly ovate to rounded with a straight margin along capsule axis.

Thailand.— SOUTH-WESTERN: Prachuap Khiri Khan [Khao Sam Roi Yot National Park, ∂ fl. 13 July 1924, *Kerr* 10978 (holotype K!; isotypes BK!, BM!,); idem, ∂ fl. 8 Aug. 1966, *Larsen et al.* 1257 (AAU); Khao Sam Roi Yot National Park, Pak Tawan, ∂ fl. 29 July 1931, *Kerr* 20512 (BK, BM, K); Khao Sam Roi Yot National Park, trail from Tham Sai to Tham Phraya Nakhon, 12° 11' N, 100° 01' E, ∂ fl. 18 Aug. 2002, *Middleton et al.* 1181 (BKF, GH, K); idem, 12° 10' 53.9" N, 100° 00' 9.8" E, ♀ fr. 2 Dec. 2002, *Thapyai & Wilkin* 509 (BK, BKF, PNU); Khao Sam Roi Yot National Park, Khao Khan Bandai, Ban Na Thung, 12° 16' 7.3" N, 99° 56' 22.4" E, ∂ fl. (old) 3 Dec. 2002, *Thapyai & Wilkin* 514 (BK, BKF, PNU); idem, ♀ fr. 3 Dec. 2002, *Thapyai* 513 (BK, BKF, PNU, QSBG)].

Distribution.— Restricted to Khao Sam Roi Yot National Park, Prachuap Khiri Khan Province.

Ecology.— In open vegetation on and around rocky limestone hills and outcrops, from near sea level to about 150 m. Flowering July to August, fruiting October to December. The flowering period is early in the year; most Thai yams from north of the Isthmus of Kra have their peak flowering period in September and October. This is probably a response to water availability at Khao Sam Roi Yot declining rapidly once the rains stop, necessitating early fruit development.

Vernacular.— Man nok (มันนก) (Prachuap Khiri Khan) (Man Tam Rak according to Prain & Burkill (1936), in error).

Conservation.— An endemic of very restricted range. During the 2002 fieldwork one apparently small population (less than five plants seen) was found on the trail from Tham Sai to Tham Phraya Nakhon and a second larger one of about 20 plants at Khao Khan Bandai, Ban Na Thung. Of course, *D. inopinata* may occur on many of the other "300 hills" of Khao Sam Roi Yot National Park. The protection afforded by the park should assure its future. IUCN red list category VU D1 (IUCN 2001).

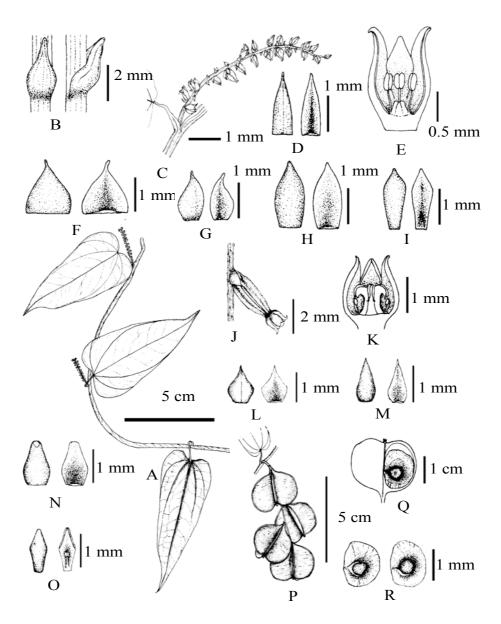


Figure 1. *Dioscorea inopinata* Prain & Burkill: A. plant habit and male inflorescences; B. cataphyll; C. a simple, spicate male inflorescence; D. male primary bract dorsal and ventral surfaces; E-I. male flower; E. longitudinal section showing stamens and pistillode; F. floral bract dorsal and ventral surfaces; G. bracteole dorsal and ventral surfaces; H. outer tepal dorsal and ventral surfaces; I. inner tepal dorsal and ventral surfaces; J-O. female flower; J. side view with ovary; K. longitudinal section (excluding ovary) showing staminodes, style and stigmas; L. floral bract dorsal and ventral surfaces; M. bracteole dorsal and ventral surfaces; N. outer tepal dorsal and ventral surfaces; O. inner tepal dorsal and ventral surfaces; P. infructescence; Q. mature capsule, longitudinal section showing seed position; R. seeds. A, C from *Kerr* 10987; B from *Kerr* 20512; D-I from *Middleton et al.* 1181; J-R from *Thapyai & Wilkin* 513. Drawn by C. Thapyai.

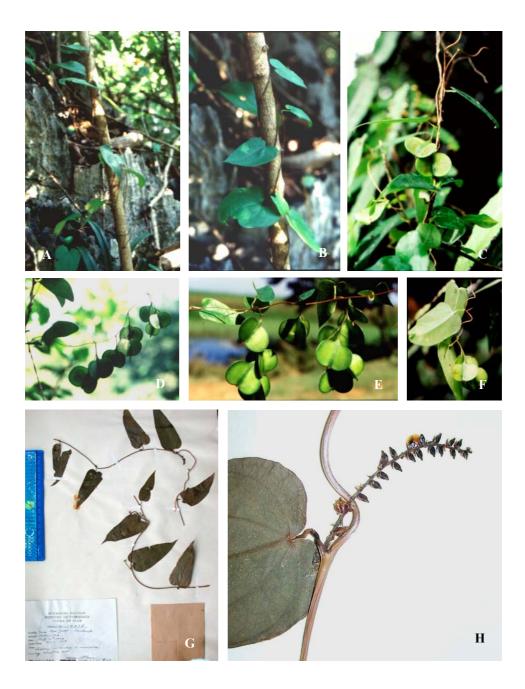


Figure 2. *Dioscorea inopinata* Prain & Burkill: A–B. habit, showing right-twining stem, short petioles and alternate leaf arrangement. C–F. capsules, showing the short, few-fruited infructescences. G–H. the holotype specimen at K. (*Kerr* 10978), showing the spicate male inflorescence and elliptic-oblong tepals. Photographed by C. Thapyai.

Notes.— The distinguishing characters of *D. inopinata* are leaves with very short petioles and alternate leaf arrangement on right-twining stems. The male inflorescence axis does not exceed 2.6 cm long, and its flowers are held more or less patent to the axis. The tepals of both sexes are elliptic-oblong and the female infructescences are not more than 8 cm long, bearing five capsules at most. The tubers of *D. inopinata* remain unknown; like those of all limestone species, they are difficult to obtain.

DISCUSSION

Critical evaluation of the morphological character data now available for *D. inopinata* suggests that it is a member of *D.* sect. *Enantiophyllum* and not related to *D. bulbifera*. This conclusion is based on the information in Table 1. The systematically important characters of the three taxa are given, and an attempt has been made to look for synapomorphies using the phylogenetic trees of Wilkin et al. (submitted) based on plastid gene sequence data. This shows that *D. inopinata* shares just one apparent synapomorphy with *D. bulbifera*, its tepal shape. However, *D. inopinata* does not have the unique tepal coloration of *D. bulbifera*, and the apex shape is different, suggesting that this similarity is non-homologous and probably convergent (as indicated by * and **). *D. inopinata* lacks all of the other autapomorphies of *D. bulbifera*, but shares right-twining with *D.* sect. *Enantiophyllum*. Its placement in *D.* sect. *Enantiophyllum* is also supported by Wilkin et al. (submitted). A hybrid origin remains possible, but it seems unlikely given that the main apomorphic characters of *D. bulbifera*; bulbil formation, the typical semicircular, membranous lateral nodal flange (Wilkin, 2001) and an oblong capsule are not encountered at all in *D. inopinata*.

Table 1. A comparison of the morphological characters of *D. inopinata* with *D.* sect. *Enantiophyllum* and *D. bulbifera.** = probable synapomorphy/autapomorphy. Polarity decisions are based on the tree topology of Wilkin et al. (submitted).

Character	D. inopinata	D. sect. Enantiophyllum	D. bulbifera
Stem twining direction	RH*	RH*	LH
Leaf arrangement	Alternate	Opposite (usually)*	Alternate
Lateral nodal flange	Absent	Absent	Present*
Bulbil formation	Absent	Rare	Present*
Tepal shape	Elliptic-oblong to lanceolate, apex obtuse to acuminate*	Ovate to orbicular, apex usually obtuse to rounded	Elliptic-oblong, apex obtuse**
Tepal colour	Green-yellow	Pale green to green- yellow	Pale green (immature), cream- yellow (at anthesis), purple to red-brown (post anthesis)*
Capsule shape in outline	Broadly obovate	Orbicular or broadly obovate to transversely elliptic-oblong	Oblong*
Seed wing	All around seed margin	All around seed margin	Basal on seed only*

Dioscorea inopinata shows interesting similarities with other D. sect. Enantiophyllum species found on limestone in Thailand. All are plants of relatively low stature, with small, narrow leaves and wiry stems to reduce evapotranspitration, due to the low water availability on limestone substrates. The narrowest leaves are encountered in D. calcicola Prain & Burkill, where they can be alternate or opposite, and D. gracilipes Prain & Burkill, where they are always opposite. Both are from Peninsular Thailand and have the typical ovate to orbicular tepal shape of the section, with obtuse to rounded tepal apices. D. depauperata Prain & Burkill is a member of the D. alata L. group (with flexuous male inflorescences) of Prain & Burkill (1936), and has alternate leaves at its stem base and shoot apices. Its tepals are also typical of D. sect. Enantiophyllum; it is found in Kanchanaburi Province, and possibly also in Laos. D. stemonoides Prain & Burkill has leaves which are alternate at the stem base and typical D. sect. Enantiophyllum tepals. It is distributed sparingly in Central, eastern and northern Thailand. Both D. stemonoides and D. depauperata have similar small, ovate or narrowly ovate leaves with a shallow basal sinus like D. inopinata; the former may well be its closest relative. Possessing alternate leaves to some degree allows these species to further reduce water loss and suggests that in D. inopinata this adaptation has progressed to a greater degree than in the other species. It is also noteworthy that all five species (with occasional exceptions e.g. Middleton et al. 1181) produce few small, simple male inflorescences and few-fruited infructescences. D. inopinata is probably the most extreme example of this trait. In limestone substrates, nutrients are limited both by the lack of soil and the lack of water to carry them. Therefore there is little investment in reproduction compared with non-limestone species, especially in relatively expensive female organs. In terms of future work, detailed studies of the autecology, including the reproductive biology, of D. inopinata are highly desirable, particularly to help to conserve this rare endemic species.

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