Dioscorea orbiculata Hook. f. and D. tenuifolia Ridl. in Peninsular Thailand and stellate hairs in D. sect. Enantiophyllum Uline

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ABSTRACT. Dioscorea sect. Enantiophyllum Uline is characterised by possession of right-twining stems. Most species have opposite leaves and are (sub)glabrous. Only one Asian species, D. orbiculata Hook. f., has stellate or dendroid pubescence. Five African species with the same combination of characters have been classified as a separate section, D. sect. Asterotricha Uline. A comparative morphological study has led to the reduction of the subglabrous D. tenuifolia Ridl. to varietal status within D. orbiculata. This new concept of D. orbiculata possesses a range in indumentum from a few unbranched hairs on young buds to dense stellate or dendroid hairs. It supports the hypothesis that all species of Dioscorea in the Old World which twine to the right should be placed in D. sect. Enantiophyllum, rather than infrageneric taxa being separated based on possession of stellate pubescence.

INTRODUCTION

Dioscorea sect. Enantiophyllum Uline is readily recognised by its right-twining habit, usually accompanied by opposite leaves. Most of its species are wholly glabrous or hairy only on very young axillary buds. According to Prain & Burkhill (1938) only 10 of the ca. 120 species possess significant pubescence, all 10 being from Asia and Australasia. Species from Africa of the section, as defined by Burkhill (1960), are all glabrous (Burkill 1939, Milne-Redhead 1975, N’Kounkou 1993, Wilkin 2001).

Dioscorea orbiculata Hook. f. from the Malay peninsula and Sumatra is the only Asian yam species with right-twining stems, opposite leaves and stellate or dendroid pubescence (Burkill 1951). It appears to be very easy to identify through its indumentum, though the character seems to have been neglected by Prain & Burkhill (1938) despite being stated to be the main feature distinguishing it from the widespread South east Asian species D. pyrifolia Kunth in its protologue (Hooker 1892). Even Burkill (1951) downplayed the use of the pubescence as a character and stated that only the larger hairs are dendroid, suggesting that D. orbiculata has both simple and dendroid hairs.

In Africa there are five right-twining, opposite-leafed Dioscorea species with stellate hairs, including the common and widespread D. schimperiana Hochst. ex Kunth and D. hirtiflora Benth. Knuth (1924) placed the African right-twiners with stellate hairs in two sections, D. sect. Syntepalia Uline (including D. hirtiflora) and D. sect. Asterotricha

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At the outset of research towards a Flora of Thailand account for Dioscoreaceae, *Dioscorea orbiculata* was known from two Kerr collections from Peninsular Thailand, respectively from La-un and Betong (Prain & Burkill 1938). Burkill (1951) stated that it was common further south. *Dioscorea tenuifolia* Ridl., which is found in Sumatra and Singapore, has a very similar vegetative morphology but is wholly glabrous and has positively geotropic (pendent) male partial inflorescences (Prain & Burkill 1938, Burkill 1951). Specimens have recently been examined which appear to be attributable to these taxa and a third pubescent, right-twining species in Peninsular Thailand, *D. pyrifolia* (also a member of *D.* sect. *Enantiophyllum*). Thus the morphology of specimens from Thailand and more southerly localities has been studied to investigate the limits of these three species. The remaining pubescent species of *D.* sect. *Enantiophyllum*, which are mainly from South Asia, appear more closely related to the Thai species, *D. decipiens* Hook. f. The exception to this is *D. polyclades* Hook. f. from Peninsular Malaysia, which resembles *D. pyrifolia* but has unique short, dense male partial inflorescences in which the axis is concealed by the flowers and floral bracts.

**MATERIALS & METHODS**

The Dioscoreaceae treatment for the Flora of Thailand is based on examination of 1220 specimens from Thailand from the following herbaria: AAU, B, BK, BKF, BM, CMU, E, K, L, P, Biology Department, Naresuan University, Phitsanulok (PNU) and QBG. Abbreviations (except PNU) follow Holmgren & Holmgren (1990). In this study it was supplemented by specimens from other parts of South and Southeast Asia at K. Comparative morphology was used to delimit species in all cases.

**RESULTS**

Table 1 is a comparison of the morphological characters which differentiate *D. orbiculata*, *D. pyrifolia* and *D. tenuifolia*. It shows that *D. pyrifolia* differs from the other two taxa in its pubescence, the habit of its male partial inflorescences, the shape of its male floral buds, the size of its male floral tepals and seed wing. These differences can also be seen in Figs. 4 and 5. It should also be noted that *D. pyrifolia* has a different ecology; it is always found in wet but open habitats, for example by rivers or in swamp forest (where it is found in Narathiwat province). *Dioscorea orbiculata* and *D. tenuifolia* occur in forest on slopes with well-drained soils. Furthermore, the tubers of *D. pyrifolia* are not eaten, unlike those of the other two taxa. Thus *D. pyrifolia* appears to be a distinct species. Female plants of *D. pyrifolia* are readily distinguished through their pubescence.

By contrast, the vegetative and reproductive morphologies of *D. orbiculata* Hook.f. and *D. tenuifolia* Ridl. are similar (see Figs 1–3). The shapes and size ranges of all parts overlap, although female flowers of *D. tenuifolia* were not available for study.
They also both occur in evergreen forest on slopes. The only consistent difference between them is that *D. orbiculata* has stellate or dendroid pubescence, especially on young growth. The species is glabrescent, but the hairs persist around nodes, on petiole bases and apices, on the veins of leaf lower surface towards point of petiole insertion and on inflorescence axes. *Dioscorea tenuifolia* is almost glabrous, but does have simple hairs on very young axillary buds. Simple hairs also appear to be present to some degree on very young axillary buds in *D. orbiculata*. Thus *D. tenuifolia* should be regarded as a variety of *D. orbiculata* and is sunk into that species below. It appears that this is a single species which can possess stellate, dendroid or simple hairs. Burkill (1951) noted that *D. tenuifolia* with large leaves is very similar to *D. orbiculata*. The species as a whole is found in South western and Peninsular Thailand. Malaysia and Sumatra, but var. *orbiculata* has not yet been encountered in Peninsular Thailand. The two specimens from Thailand determined by Burkill as *D. orbiculata* were misidentified and referable to *D. pyrifolia* (Kerr 16514, from La-Un near Ranong) and *D. orbiculata* var. *tenuifolia* (Kerr 16584, from Betong in Yala Province). *D. orbiculata* var. *orbiculata* has been collected close to the Thailand-Malaysia border at Penang Island and Sungai Larut in Perak Province (specimens at K) and Langkawi in Peninsular Malaysia (according to Prain & Burkill 1938), so it is likely that there are some populations in Thailand.

**DESCRIPTION**


*Climber* to 10 m in height. *Underground parts* unknown in Thai specimens, according to Burkill (1951) tuberous, with several tubers produced each year at the end of long spreading or descending stalks, crown woody (Fig. 2M), parenchyma white, edible. *Stems* 7–10 mm in diam. towards base, 1.5–6 mm in diameter on upper stems, twining to the right, annual, towards base woody and bearing paler prickles (Fig. 1D, 2N, 3C), nodes often swollen and densely prickly, unarmed on upper stem, terete, pale green to dark green in colour. *Leaves* simple, opposite, sometimes subopposite to alternate towards stem base, blade 2.8–12.5 by 3.0–10.1 cm, lanceolate or elliptic-oblong to ovate, ovate-oblong to broadly so or orbicular, 5–7-nerved, only main vein and first vein pair reaching apex; chartaceous, yellow-green to dark green above, paler below, drying olive- or grey-green, darker above, base cordate to cuneate, sinus (where present) to 10 mm deep, apex 2–6 mm long, acuminate, margin entire; forerunner tip drying brown to dark brown; *petioles* 2.1–10.5 cm long, terete, shallowly channelled above, coloured as stem; *cataphylls* (Figs. 1D and 3B) 5–8 by 3–12 mm, broadly ovate, often prickly on dorsal surface, texture like prickles, apices 2.5–7 mm long, acuminate; *nodal prickles* present or absent; *bulbils*
absent. *Inflorescences* spicate, axes slender, terete, coloured as stem, all bracts chartaceous; tepals inserted on discoid torus, free, ventrally concave, fleshy in texture, greenish-yellow to pale yellow, apex cucullate. *Male inflorescences* (Fig. 2A, 2B, 3A, 3D) simple or compound, compound inflorescences 5–30(–45) cm long, 1–2 per axil; primary bracts (Fig. 2D, 3F) 3–3.6 by 0.8–1 mm, narrowly lanceolate to lanceolate-oblong or ovate, apices acuminate, 0.6–0.8 mm long; simple/partial inflorescences 1–3 (–5) per axil, positively geotropic (pendent), with all partial inflorescences orientated above a line at right-angles through axis node (Fig. 2A, B, 3A) in herbarium specimens, peduncles 1.8–6(–10) mm long, axes 2.5–13 cm long. *Female inflorescences* (Fig. 1A) simple, pendent, 1 per axil, peduncles 1–2.5 cm long, axes (1.8–)3–13 (–20) cm long; flowers orientated at an angle of 30°–80° to axis when receptive. *Flowers* with erect tepals which are apically incurved-cucullate leaving only a small apical opening, inserted on a small, flat or weakly convex torus. *Male flowers* conical in bud (at least in dried material) with floral bracts (Fig. 2D, F, 3E, I) 0.6–0.9 by 0.4–0.8 mm, ovate to broadly ovate, apices 0.1–0.6 mm long, acuminate; bracteoles (Fig. 2G) 0.5–0.7 by 0.4–0.6 mm, ovate, apices 0.1–0.25 mm long, acuminate; outer tepals (Fig. 2H, 3L) 1.0–1.2 by 0.8–1.3 mm, ovate to ovate-oblong, apex acute to obtuse; inner tepals (Fig. 2I, 3L) 0.9–1.1 by 0.5–0.7 mm, narrowly ovate, apex obtuse; stamens 6 (Fig. 2E, 3H), inserted on torus, filaments 0.1–0.25 mm long, anthers 0.2–0.35 by 0.1–0.25 mm, ovate to ovate-oblong; pistilodes 3 (Fig. 2E, 3H), 0.1–0.15 by 0.05–0.1 mm, erect, inner surfaces contingent. *Female flowers* with floral bracts (Fig. 1H) 0.8–1.5 by 0.9–1.2 mm, ovate to broadly ovate, apices short-acuminate; bracteoles (Figure 1I) 0.6–0.9 by 0.6–0.8 mm, ovate, apices 0.05–0.15 mm long, acuminate; outer tepals (Fig. 1J) 0.6–1.1 by 0.6–1.1 mm, ovate to obovate or broadly so, apex obtuse; inner tepals (Fig. 1K) 0.6–0.8 by 0.4–0.8 mm, ovate to obovate, apex obtuse; ovaries (Fig. 1E) 3.7–4.8 by 1.5–3.1 mm, narrowly oblong to elliptic in outline; staminodes 6 (Fig. 1F, 1G), 0.15–0.3 mm long, staminiform, inserted on tepal bases; styles (Fig. 1G) 0.2–0.3 by 0.3–0.4 mm, fused for two-thirds of their length to form an erect column; stigmas (Fig. 1F, 1G) 0.2–0.3 mm long, deeply bifid, recurved. *Infructescences* (Fig. 2J) 8–15 cm long; capsules (Fig. 2K) 24–28 by 36–47 mm, obovate to broadly obovate in outline, base truncate, apex retuse, sinus 0.1–3 mm deep, capsular stipes 6–8 by 4.5–7 mm, obconic; immature capsules pale green to mid-green; mature capsules deflexed at an angle of 30°–60° to axis, dehiscence of each lobe controlled by a marginal strip (Fig. 2K). *Seeds* (Fig. 2L) 5–5.5 by 3–3.5 mm, lenticular-ovoid; wings 19–21 by 15–17 mm, extending all around seed margin, broadly ovate to rounded with a straight edge along capsule axis.

**var. orbiculata**

Plant pubescent, indumentum present on all parts except inner whorl tepals, hairs predominantly or completely stellate or dendroid (Fig. 1B, C), 0.15–0.35 mm long, brown to red-brown or grey, usually dense on young shoots, at nodes, on petiole bases and apices and veins of leaf lower surface towards point of petiole insertion and inflorescences, sparse to absent elsewhere with age; some simple hairs on very young axillary buds. Leaves ovate or ovate-oblong to broadly so or orbicular, base shallowly cordate to rounded; nodal prickles often present towards stem base, 2–2.5 mm long, straight or curved; cataphylls often prickly on dorsal surface (Fig. 1D).
Dioscorea orbiculata Hook. f. and D. tenuifolia Ridl. in Peninsular Thailand

Distribution.— Peninsular Malaysia and Indonesia (Sumatra), the latter according to Prain & Burkill (1938). Possibly also in Southern Peninsular Thailand.

Ecology.— Moist evergreen forest between 50 and 300 m elevation. Flowering August–January, fruiting November–February.

Vernacular name.— Not known.

Uses.— Tuber edible, presumably cooked (Prain & Burkill 1938).

Conservation.— Least concern (LC) (IUCN 2001).

Notes.— The lectotype above was chosen because it is the most complete and representative of the two specimens cited by Hooker in the protologue; *Philipps* s.n. has immature flowers.

var. **tenuifolia** (Ridl.) Thapyai, **comb.nov.**


All parts of plant glabrous except very young axillary buds with dense, simple pubescence. Leaves lanceolate or elliptic-oblong to broadly ovate, base cuneate to truncate; nodal prickles and cataphyll prickles absent. Male inflorescences sometimes damaged by galls (Fig. 3D).


Distribution.— Peninsular Malaysia, Singapore (Type), Sumatra (according to Prain & Burkill 1938) and Peninsular Thailand.

Ecology.— Moist evergreen forest between 50 and 200 m elevation. Flowering August–January, fruiting November–February.

Vernacular name.— Man ta yong (มันตาหยง) (Yala).

Uses.— Tuber edible, presumably cooked (Burkill 1951).

Conservation.— Least concern (LC) (IUCN 2001). Collections of var. *tenuifolia* are less numerous than those of var. *orbiculata*, but it appears to be common in Singapore and occurs over a wide area. It is probable that it occurs sporadically throughout the range of var. *orbiculata*.

Notes.— The protologue of this species gives its name as *D. tenuifolia* in error (see Prain & Burkill 1938).
It is not clear why Prain & Burkill (1938) placed *Dioscorea repanda* Blume in synonymy with both this species and *D. prainiana* R. Knuth. No type was cited by Blume (Enum. Pl. Javae 1: 22 (1827) or by Kunth (Enum. Pl. 5: 400 (1850)) and Blume clearly states that his plant is from Java, whereas *D. tenuifolia* is only found on Sumatra. *Dioscorea prainiana* is also found in the Malay Peninsula and Sumatra. It appears that *D. repanda* Blume cannot be assigned satisfactorily to any taxon. *Dioscorea prainiana* differs from *D. orbiculata* through its tubers lacking stalks and possessing negatively geotropic (i.e. erect) male partial inflorescences, with male flowers which are held patent to the axis. In *D. orbiculata* the male flowers are orientated towards the apex of the partial inflorescence and appear to make an angle of ca. 45° to it, especially in the bud stage. The tepals of *D. prainiana* are not held together as tightly as those of *D. orbiculata*, which have a very small opening at the apex (Fig. 2D, 3E, H). These characters suggest that *D. prainiana* may have a different and larger pollinator. *Dioscorea prainiana* also appears to lack hairs even on the buds, making it possible to identify female or sterile material.

**DISCUSSION**

The existence of a species with both almost glabrous individuals and others with stellate hairs suggests that pubescence characters should be used with care to separate species within *D. sect. Enantiophyllum*. Knuth and Burkill were wrong to separate *D. sect. Syntepalia* and *Asterotricha*; all right-twining and opposite leafed Old World species of *Dioscorea* are best referred to a single section. This conclusion is also supported by molecular data, with *D. schimperiana* falling sister to rest of *D. sect. Enantiophyllum* (Wilkin et al., 2005). The combination of these sections makes this the most diversified Old World infragenERIC group with over 80 species. Species limits in this section are often complex and it needs monographic and phylogenetic study, in particular because it contains the most important Asian and African starch-providing yams and their relatives.

**ACKNOWLEDGEMENTS**

CT would like to express his gratitude to the QBG - DANCED Program for granting the scholarship for conducting research and study at the Faculty of Forestry, Kasetsart University. We thank all the Royal Forest Department staff who helped us. Research on Thai Dioscoreaceae was made possible by all the herbarium curators who gave access to specimens through loans, visits or electronic means. Thanks also to Phillip Cribb for constructive comments on an earlier version of this manuscript.

**REFERENCES**


Table 1. A comparison of the morphological characters which differentiate *D. orbiculata*, *D. pyrifolia* and *D. tenuifolia*

<table>
<thead>
<tr>
<th>Character</th>
<th><em>D. orbiculata</em></th>
<th><em>D. pyrifolia</em></th>
<th><em>D. tenuifolia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Underground part (Prain &amp; Burkill, 1938)</td>
<td>Tuber deeply buried, spreading, on long stalks with arise from a woody knot, (Fig.2N), edible.</td>
<td>Tuber several, buried to 2.5 m deep on long stalks below a woody knot, (Fig.5K), not eaten.</td>
<td>Tuber several, descending into the soil, on long stalks under a woody knot, edible.</td>
</tr>
<tr>
<td>Indumentum</td>
<td>Hairs predominantly or completely stellate and dendroid (Fig. 1B,C), glabrescent but remaining dense at nodesm on petiole bases and apices and vein of leaf lower surface towards point of petiole insertion, some simple hairs on very young axillary buds.</td>
<td>Hairs all stiletto-shaped (Fig.4B,i.e. with four spheroidal projections at the hair base ), glabrescent but remaining dense at nodes, on petiole base and apices and vein of leaf lower surface towards point of petiole insertion.</td>
<td>Glabrous except very young buds with dense, simple hairs.</td>
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<tr>
<td>Leaf blade shape/colour when dry</td>
<td>Ovate or ovate-oblong to broadly so or orbicular, base shallowly cordate to rounded, drying olive- or grey-green, darker above.</td>
<td>Lanceolate or narrowly ovate-deltoid to ovate, ovate-oblong, or elliptic-oblong, base cordate or sagittate to truncate, often drying red-brown, especially lower surface and veins.</td>
<td>Lanceolate or elliptic-oblong to broadly ovate, base cuneate to truncate, drying olive- or grey green, darker above.</td>
</tr>
<tr>
<td>Male partial inflorescences habit</td>
<td>Positively geotropic (pendent); in herbarium specimens all partial inflorescences orientated above a line at right-angles through axis node (Fig. 2A,B)</td>
<td>Little or no geotropism-partial inflorescences produced at all angles around axis node (Fig.4A)</td>
<td>Positively geotropic (pendent); in herbarium specimens all partial inflorescences orientated above a line at right-angles through axis node (Fig. 3A)</td>
</tr>
<tr>
<td>Male floral bud shape (in dry material)</td>
<td>Conical</td>
<td>Globose to ovoid</td>
<td>Conical</td>
</tr>
<tr>
<td>Male tepal dimension (mm)</td>
<td>1.0-1.2 by 0.8-1.3 (outer) 0.9-1.1 by 0.5-0.7 (inner)</td>
<td>0.8-0.9 by 0.6-0.7 (outer) 0.6-0.8 by 0.4-0.6 (inner)</td>
<td>1.0-1.2 x 0.8-1.3 (outer) 1.0-1.1 x 0.5-0.6 (inner)</td>
</tr>
<tr>
<td>Seed wing dimension (mm)</td>
<td>19-21 by 15-17</td>
<td>20-22.5 by 19-22</td>
<td>15-17.5 x 15-16</td>
</tr>
</tbody>
</table>
Figure 1. *Dioscorea orbiculata* var. *orbiculata*; vegetative and female floral organs: A. habit, with female inflorescence; B. dendroid hairs; C. stellate hairs; D. prickly (left) and unarmed (right) cataphylls, dorsal and side views; E.–K. female flower; E. side view, showing tepals, ovary, position of floral bract and bracteole and insertion onto inflorescence axis; F. top view, tepals opened for drawing; G. half flower showing staminodes, style and stigmas; H. floral bract, dorsal and ventral view; I. bracteole, dorsal and ventral view; J. outer tepal, dorsal and ventral view; K. inner tepal, dorsal and ventral view; A.–C., E.–L. from *Burkill & Mohammed Haniiff* 16077; D. from *Burkill* 6316. Drawn by C. Thapyai.
Figure 2. *Dioscorea orbiculata* var. *orbiculata*; male reproductive organs, underground parts, stem base and fruit: A. compound male inflorescences in axils of opposite leaves; B. simple male inflorescences; C. primary bract from compound male inflorescence; D. part of male partial inflorescence showing floral bracts and insertion onto axis; E.–J. male flower; E. half-flower 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. infructescence; K. mature capsule with dehiscent capsular strips, longitudinal section showing position of two seeds in locule; L. seeds showing wings; M. underground organs with woody crown (on left); N. stem base showing prickles. A., B. from Wray 1255; C.–I. from Burkill & Mohammed Haniff 16076; J.–N. from Henderson s.n. Drawn by C. Thapyai.
Figure 3. *Dioscorea orbiculata* var. *tenuifolia*: A. habit, with compound male inflorescence; B. cataphyll, dorsal and side view; C. stem base with spines; D. male partial/simple inflorescence with galled flowers (commonly observed this variety); E. part of male partial inflorescence showing insertion of flower onto axis and floral bract position; F. primary bract of male partial inflorescence; G.–L. male flower; G. top view, tepals opened for drawing; H. half flower, showing stamens and pistillode; I. floral bract dorsal and ventral view; J. bracteole dorsal and ventral view; K. outer tepal dorsal and ventral view; L. inner tepal dorsal and ventral view; M. two infructescences; N. immature capsule, longitudinal section showing position of two seeds in locule; O. immature seeds with wings; A., D., E.–L. from Sangkhachand 1548; B. from Mohammed Nur 2422; C. from Mohammed Nur 4181; M.–Q. from Ridley 13319. Drawn by C. Thapyai.
Figure 4. *Dioscorea pyrifolia* Kunth male plant: A. habit with compound inflorescences; B. “stiletto” hairs; C. cataphyll; D. part of partial inflorescence; E. primary bract dorsal and ventral surfaces; F.–L. male flower; F. view from above, tepals opened; G. longitudinal section showing stamens and pistillodes; H., I. floral bract and bracteole dorsal and ventral surfaces respectively; J., K. outer and inner tepal dorsal and ventral surfaces respectively. A., D.–K. from Wilkin 826; B., C. from Wilkin 823. Drawn by C. Thapyai.
Figure 5. *Dioscorea pyrifolia* Kunth female plant: A.–E. female flower; A. side view; B. longitudinal section (excluding ovary) showing staminodes, style and stigmas; C., D. floral bract and bracteole dorsal and ventral surfaces respectively; E., F. outer and inner tepal dorsal and ventral surfaces respectively, showing position of staminode insertion; G. part of infructescence; H. mature capsule, longitudinal section showing seed position in locule; I. seeds; J. underground organs showing spiny stem bases, long slender tuber stalks (proximal part only) and thick roots of woody crown; A.–F. from *Mohammed Nur* 32956; G.–J. from *Mohammed Nur* 32652; K. from *Wilkin* 823. Drawn by C. Thapyai.