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DISCHIDIA (APOCYNACEAE, ASCLEPIADOIDEAE) IN LAOS AND VIETNAM

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SUMMARY

Two new species, *Dischidia dohtii* Tran & Livsh. and *D. cornuta* Livsh., are described and illustrated. *Dischidia rimicola* Kerr is illustrated for the first time. All three species are associated with tree-nesting ants of the genus *Crematogaster*. Presentation experiments with seeds of *D. rimicola* indicate that they are attractive to the ants. The possible affinity between *D. dohtii* and the enigmatic *D. khasiana* Hook.f. from north-eastern India is discussed; *D. khasiana* is lectotypified. A key to the 14 species of *Dischidia* documented from Vietnam and Laos and a list of exsiccatae are provided.

Key words: *Dischidia*, Apocynaceae, Asclepiadaceae, morphology, taxonomy, ecology, ant plant.

INTRODUCTION

The genus *Dischidia* R.Br. comprises approximately eighty species of epiphytic vines in Indochina, Malesia, Melanesia, and the east Pacific. Many species grow on the nests of arboreal ants (Kaufmann et al., 2001 and references therein). Species of section *Ascidophora* K. Schum. have highly modified pitcher leaves that function as ant houses (Janzen, 1974). While it has recently been the subject of floristic treatments (Rintz, 1980; Li et al., 1995; Forster et al., 1996; Jagtap & Singh, 1999) and studies of its ecological associations with ants (Treseder et al., 1995; Kaufmann et al., 2001), both the taxonomy and ecology of *Dischidia* remain poorly understood through most of its range. We made field observations on three species in the highlands of Laos, including two that are here described as new. One of these, *Dischidia cornuta*, is known only from Laos; the other, *Dischidia dohtii*, also occurs in Vietnam. The third species, *Dischidia rimicola* Kerr, was previously known only from Thailand (Kerr, 1939; Craib & Kerr, 1951) but occurs also in Vietnam and Laos. We illustrate *D. rimicola* for the first time and provide a detailed description, including the first description of its fruits and seeds.

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MATERIALS AND METHODS

Herbarium specimens from A, BH, BISH, BKF, BRIT, C, CAL, F, G, HN, K, KEP, L, M, MO, NY, P, PH, PNH, SING, UKM, and US were examined. Observations were made on living, herbarium, and alcohol preserved specimens. For SEM, flowers were preserved in FAA and stored in 70% EtOH, dissected, put through a dehydration series, critical point dried, mounted on aluminium stubs with two-sided tape, coated with gold-palladium, and viewed with a Zeiss 960 SEM. All photography is digital. Some images were re-touched to remove charge lines, debris, cracks in the background, and small nicks; re-touching did not alter the morphology or micro-morphology depicted in the images. Distribution of sclerenchyma in the anthers was determined by staining preserved or reconstituted flowers with phloroglucinol-HCl.

Seed presentation experiments were conducted at Nong Khoum Khiaou, 15.20 N, 106.32 E, 1000 m, at Thongset Village, Champasak Province, Laos in January 2000. The forest, at 1000 m, is very open and shrubby, with parts converted to agricultural land. Each experiment consisted of placing a small plastic dish with five *D. rimicola* seeds with their coma removed, five achenes of *Elephantopus* spec. (Asteraceae) of similar size and shape, and five pieces of silica gel (as an inert control) near a nest of *Crematogaster* spec. C with *D. rimicola* growing in it, and noting the time of removal of each object. Observations were stopped 10 minutes after ants removed all *Dischidia* seeds or all of one type of object. We found four accessible nests, two of these were disturbed when discovered and the ants' response to placement of the dish near their nest was to stay inside the nest (first nest) or to ignore the dish and continue transporting pupae from one part of the nest to another (second nest). Thus the experiment was conducted with two nests only.

RESULTS

ECOLOGY

Dischidia cornuta, *D. dohtii*, and *D. rimicola* grow sympatrically in an open, secondary, Fagaceae-dominated forest, at 1000 m on the Bolaven Plateau in Laos. *Dischidia rimicola* also occurs in the lower canopy of a nearby primary, closed canopy, mixed deciduous forest. *Dischidia* species are much more visible at the first site but relative abundance in the two habitats is unclear without surveying the canopy of the second. *Dischidia cornuta* and *D. dohtii* are associated with *Crematogaster* spec. A (*Livshultz 00-31, 00-34*); *D. rimicola* was collected from the nests of *Crematogaster* spec. B (*Livshultz 00-20*) and *Crematogaster* spec. C (*Livshultz 00-22, 00-27, 00-29,* all ant specimens deposited at Cornell Entomological Museum). No ants were found on the plant collected from the primary forest. Because *D. rimicola* grows from a single root stock, the ant nest was easily located, in a knot in the host tree. Larvae and pupae were distributed among the roots of a plant pulled from a nest. *Dischidia cornuta* and *D. dohtii* form large mats on the host tree. Ants were abundant on the plants, but the nests were not located. No larvae or pupae were found on the branches removed for specimens.

In presentation experiments of *D. rimicola* seeds, *Crematogaster* spec. C removed all *D. rimicola* seeds but took only one *Elephantopus* spec. achene and none of the silica gel pieces (Fig. 1). We did not observe the final location of all of the objects removed,

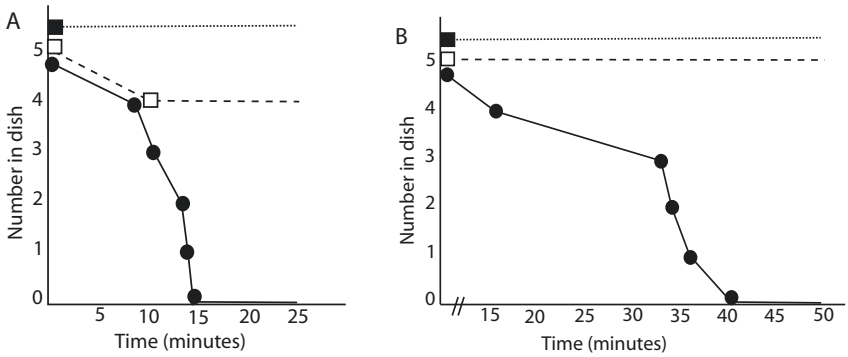

Fig. 1. Ants preferentially removed *Dischidia rimicola* seeds compared with *Elephantopus* spec. achenes in two *Crematogaster* spec. C nests tested (p = 0.05 in nest A and p = 0.005 in nest B in one-tailed Mann-Whitney U tests). We placed five *D. rimicola* seeds (filled circles) *Elephantopus* spec. achenes (unfilled squares) and silica grains (filled squares) in a small plastic dish near each nest.

but in both experiments we observed ants carrying *Dischidia* seeds into the nest. The trivial explanation for these observations is that *Elephantopus* spec. achenes are distasteful to ants. But the combination of these observations with the spacial association of *D. rimicola* with ant nests, supports the hypothesis that the *Dischidia* seeds are attractive to ants, and that this attractiveness is the basis of the ant/plant association.

Our observations agree with both experimental and informal observations of other *Dischidia* species (Kaufmann et al., 2001 and references therein; Kleijn & Van Donkelaar, 2001). A phylogenetic analysis of *Dischidia* (Livshultz, 2003a) shows that the occurrence of ant-associations is widespread in the genus and not limited to any single clade. Many species of *Hoya*, the sister genus of *Dischidia*, also form ant associations (Kaufmann et al., 2001 and references therein; Kleijn & Van Donkelaar, 2001). The wide distribution of ant-associations in *Dischidia* and *Hoya* suggests that this trait could be plesiomorphic in these epiphytes. To test this hypothesis we need a well-resolved phylogeny for the two genera and ecological data from their c. 200 species. Identification of the chemical basis for the attractiveness of *Dischidia* and *Hoya* seeds to ants would allow us to better define the trait 'ant-association', make more precise hypotheses about the homology of this trait between the two genera, and perhaps (depending on the lability of the chemicals) permit us to assay seeds from herbarium specimens of species for which there are no field observations.

TAXONOMY

A total of 14 species of *Dischidia*, thirteen native and one cultivated, are documented by herbarium specimens from Vietnam and Laos (Table 1). Of the native species, five are recorded from both countries, seven are recorded from Vietnam but not Laos, and one is recorded from Laos but not Vietnam. Given the paucity of collections, especially from Laos, it is likely that most of these species actually occur in both countries. Six of these species occur in both Indochina and Malesia (Rintz, 1980) while the other seven are endemic to Indochina (Craib & Kerr, 1951; Pham-hoang, 1993), including two new species, *D. cornuta* and *D. dohtii*. A list of exsiccatae is presented.

Table 1. *Dischidia* species in Laos and Vietnam (* = endemic to Indochina).

Species	Laos	Vietnam
D. acuminata Costantin*	–	+
D. acutifolia Maingay ex Hook.f.	+	+
D. bengalensis Colebr.	–	+
D. cornuta Livsh.*	+	–
D. dohtii Tran & Livsh.*	+	+
D. griffithii Griff. ex Hook.f.*	–	+
D. hirsuta (Blume) Decne.	–	+
D. imbricata (Blume) Steud.	–	+
D. major (Vahl) Merr.	+	+
D. nummularia R.Br.	+	+
D. oiantha Schltr. (endemic to Philippines)	cultivated	cultivated
D. rimicola Kerr*	+	+
D. tonkinensis Costantin*	–	+
D. tricholoba Kerr*	–	+

KEY TO DISCHIDIA IN VIETNAM AND LAOS

1a. Root-filled pitcher leaves present. Corolla abaxially puberulous, yellow and green, longitudinally striped, with purple lobe tips . . . . . ***D. major***

b. Root-filled pitcher leaves absent. Corolla abaxially glabrous (may be papillate), white, off-white, pale yellow, pinkish, purple, with or without purple lobe tips, but never yellow and green striped 2

2a. Leaves reniform, wider than long, older leaves with adaxial surface convex, green, abaxial surface concave, purplish red; white wax chimneys on abaxial leaf surface present (for chimneys see Fig. 2C; photograph and description in Livshultz (2003b)) 3

b. Leaves orbicular, elliptic, ovate, lanceolate, obovate, spathulate, or linear, rarely (*D. dohtii*) wider than long, older leaves plano-convex, biconvex, or only slightly succulent, both surfaces green. White wax chimneys on abaxial leaf surface present or absent. 4

3a. Staminal corona lobes reduced to two minute bumps, appearing as absent . . . . . ***D. imbricata***

b. Staminal corona lobes present as two cylindrical arms, 0.2 mm long, prominent . . . . . **D. cornuta**

4a. Corolla 6–7 mm long, dark purple with pink or cream lobes, with two distinct rings of hairs adaxially, one at throat, the second below, at the level of the anthers . . . . . ***D. hirsuta***

b. Corolla up to 5 mm long, white, cream, yellowish, or pinkish, adaxially glabrous or with a single zone of hairs on lobes or at throat 5

5a. Plants lanate with hairs to 0.9 mm long. Staminal corona of minute, unstalked T-shaped lobes, sometimes appearing as absent . . . . . **D. dohtii**

b. Plants glabrous to tomentose, hairs less than 0.2 mm long. Staminal corona of prominent, stalked lobes, always evident 6

6a. Staminal corona lobes sagittate, apices obtuse or acute. Leaves and stems lacking wax chimneys, not farinose although exfoliating epicuticular wax is sometimes apparent on herbarium specimens 7
b. Staminal corona lobes anchor-shaped, apices retuse. Leaves and stems often with wax chimneys, farinose (wax may not be apparent on very young or mesic stems or on herbarium specimens where epicuticular wax has flaked off) 11
7a. Corolla lobes pubescent near middle with antrorse hairs, throat glabrous 8
b. Corolla lobes glabrous, throat with ring of hairs 9
8a. Mature stems and calyces usually glabrous, occasionally with a few hairs. Corolla 4.8–5 mm long, no longitudinal ribs on adaxial sides of corolla lobes, bases of staminal corona lobes glabrous . . . . . ***D. tricholoba***
b. Mature stems and calyces usually tomentose, stems occasionally glabrescent. Corolla 3.5–4 mm long, with longitudinal ribs on adaxial sides of corolla lobes, with prominent tufts of hairs at bases of staminal corona lobes . . . **D. rimicola**
9a. Prominent lobes on adaxial surface of corolla (corolline corona) in corolla lobe sinuses present. Staminal corona lobes fleshy, saddle-shaped, each with a prominent, transverse abaxial ridge. Pollinarium with caudicles shorter than corpuscle (see Fig. 4F for pollinarium terminology). Leaves usually obovate, occasionally elliptic . . . . . ***D. griffithii***
b. No lobes on adaxial surface of corolla (corolline corona absent). Staminal corona lobes membranous, without abaxial ridges. Pollinarium with caudicles longer than corpuscle. Leaves elliptic or lanceolate (rarely obovate). 10
10a. Inflorescence with (1–)2–5 branches (look at older inflorescences with elongate branches), each plant with some inflorescences with 3 or more branches. Peduncles 0–0.3 cm long . . . . . ***D. acuminata***
b. Inflorescences unbranched, rarely with 2 branches. Peduncles 0–3.2 cm long . . . . . ***D. acutifolia***
11a. Leaves orbicular, broadly ovate or elliptic, always less than 1.5 cm long. Corolla lobes widely divergent at anthesis, with only slightly thickened tips. Apex of staminal corona lobe entire. Fruit lanceolate, reflexed (forming a 90° angle or less with the pedicel), (1.5–)2.5–3.7 by 0.2–0.5 cm . . . . . ***D. nummularia***
b. Leaves ovate, elliptic, spatulate, obovate, or linear; almost every specimen with some leaves over 2 cm long. Corolla lobes convergent at anthesis, with prominent cucullate thickenings at tips. Apex of staminal corona lobe emarginate or with a papilla in the centre. Fruit linear, not reflexed (forming a c. 180° angle with pedicel) (may be reflexed on herbarium specimens due to distortion during pressing), (4.6–)5–7.2 by 0.2–0.3 cm 12
12a. Leaves linear, narrowly elliptic to spatulate, blades 1.8–5 by 0.2–0.7 cm, length to width ratio 3.8–16 . . . . . ***D. bengalensis***
b. Leaves broadly elliptic to obovate, blades 1.2–4.2 by 0.7–3 cm, length to width ratio 1.1–3.2(–3.7). 13
13a. Leaves predominantly elliptic, more rarely obovate, blades 1.2–3 by 0.7–1.8 cm, apex mostly obtuse or acute, rarely truncate or retuse. — Native ***D. tonkinensis***
b. Leaves predominantly obovate, rarely elliptic, blades 3–4.2 by 1–3 cm, apex often truncate to retuse, occasionally obtuse, rarely acute. — Cultivated, native to the Philippines . . . . . ***D. oiantha***

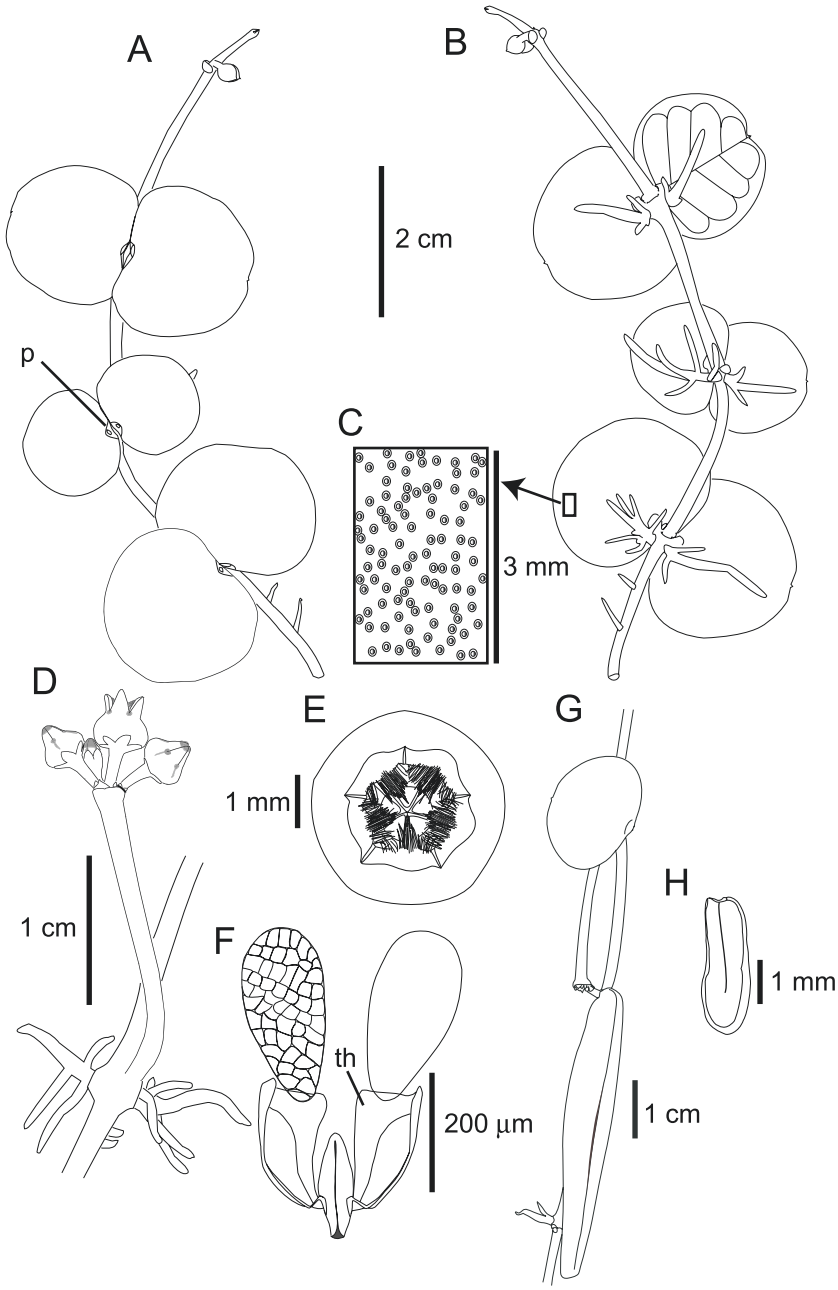

Fig. 2. *Dischidia cornuta* Livsh. A. Adaxial surface of vegetative shoot; B. abaxial surface of vegetative shoot; C. wax chimneys on abaxial leaf surface; D. inflorescence at node with aborted leaves, distribution of red pigment on corolla depicted with grey; E. flower at anthesis, viewed from above; F. pollinarium; G. shoot with infructescence; H. seed without coma (A–F: *Livshultz 02-50*; G: *Livshultz 03-40*; H: *Poilane 12136*). p = protuberance at base of leaf blade, th = thickening on the inner margin of caudicle. Drawn by T. Livshultz.

Dischidia cornuta Livsh., *spec. nov.* — Fig. 2, 3A–E

Dischidiae imbricatae affinis sed fauce corollae aperta, lobis coronae corollinis cordatis, appendicibus connectives antherarum apicem capitatis stylini tectantibus, lobis staminalibus prominentibus coronae brachiis longis praeditis, et marginibus antherarum dissimiliter formatis differens. — Typus: *Livshultz 02-50* (holo BH, iso A, L, MO, National University of Lao), cultivated, field data: Laos, Champasak Province, Ban Thongset, Nong Khoum Khiaou, 15.20 N, 106.32 E, 1000 m, 21 Aug. 2002.

Plants succulent, herbaceous, epiphytic (or epilithic fide *Poilane 12136*) vines, mat-forming root-climbers or twiners when without support. *Roots* on mature plants adventitious, always paired below each node, each root emerging opposite a leaf within 1 or 2 elongate internodes on an actively growing stem, proliferating when in contact with a suitable substrate, additional adventitious roots occasionally produced along the internodes. *Latex* white. *Indumentum* glabrous except for very sparse hairs near the margins of some younger leaves and long retrorse hairs on the corolla lobes. *Wax chimneys* present, apparent within 2 elongate internodes on an actively growing stem, most prominent on abaxial surfaces of leaves; older stems, leaves, and peduncles farinose. *Stems* terete, 1–2 mm diam., internodes 2–6 cm long; twining stems with longer internodes and reduced or aborted leaves. *Stipular colleters* paired, triangular or ovate, to 0.1 mm long, inserted on either side of each petiole. *Leaves* always opposite, decussate early in development, becoming distichous, peltate at maturity; petiole 1–2 by 1–2 mm; lamina with slightly reflexed margins early in development, concavo-convex at maturity (the adaxial surface convex and the abaxial surface concave); the abaxial side held appressed to the substrate by the adventitious roots and becoming purple with age, 1.2–2.3 by 1.5–3 cm, 1–2 mm thick, transverse ovate to reniform, apex obtuse to retuse, minutely apiculate, base truncate to slightly cordate, with a small, colleter-bearing protuberance on the adaxial side; protuberance of a mature leaf with 1 or 2 colleters, purple; venation obscure in living plant, evident on abaxial surface of herbarium specimens, brochidodromous, with 3 or 4 pairs of secondaries. *Inflorescence* extra-axillary, umbelliform or compound-umbelliform, persistent through many flowering cycles; peduncles 1–3.5 by 0.1–0.15 cm, bearing 1 or 2 condensed axes at their apices; axes 2 mm diam., elongating to 4 mm long, with extremely short internodes, each with 3 or 4 flowers and buds at various stages of maturity when actively growing, fewer flowers often observed on herbarium sheets and young or quiescing inflorescences; lower portions of axes covered with transversely elliptical scars where flowers have fallen. *Flowers* subtended by two membranous triangular to lunate bracts c. 0.5 by 0.5 mm, the bracts becoming chartaceous, persistent after flowers senesce, but wearing off from the oldest parts of the axes. *Pedicels* 3–4 by 1 mm, pale green. *Calyx* lobes quincuncial in bud, 1.5 by 0.7 mm, ovate, apex obtuse, pale green with hyaline margins, glabrous, without colleters inside sinuses. *Corolla* tube succulent, full of nectar, urceolate, 4 by 3.8 mm at widest diameter, widest 0.5 mm from the base, obscurely 5-angled, without ribs, dull pale yellow, reddish on the tips, margins, and in the sinuses of the abaxial surface of the corolla lobes, sometimes with a faint reddish stripe on the tube below each sinus, red more prominent in buds than in mature flowers. *Corolla lobes* valvate in bud, 1.5 by 0.9 mm, triangular, succulent, tips only slightly thickened, abaxially with stomate-bearing papillae, adaxially with long, straight, retrorse hairs, on tips and margins, divergent at anthesis, throat 1.5–1.8 mm diam.,

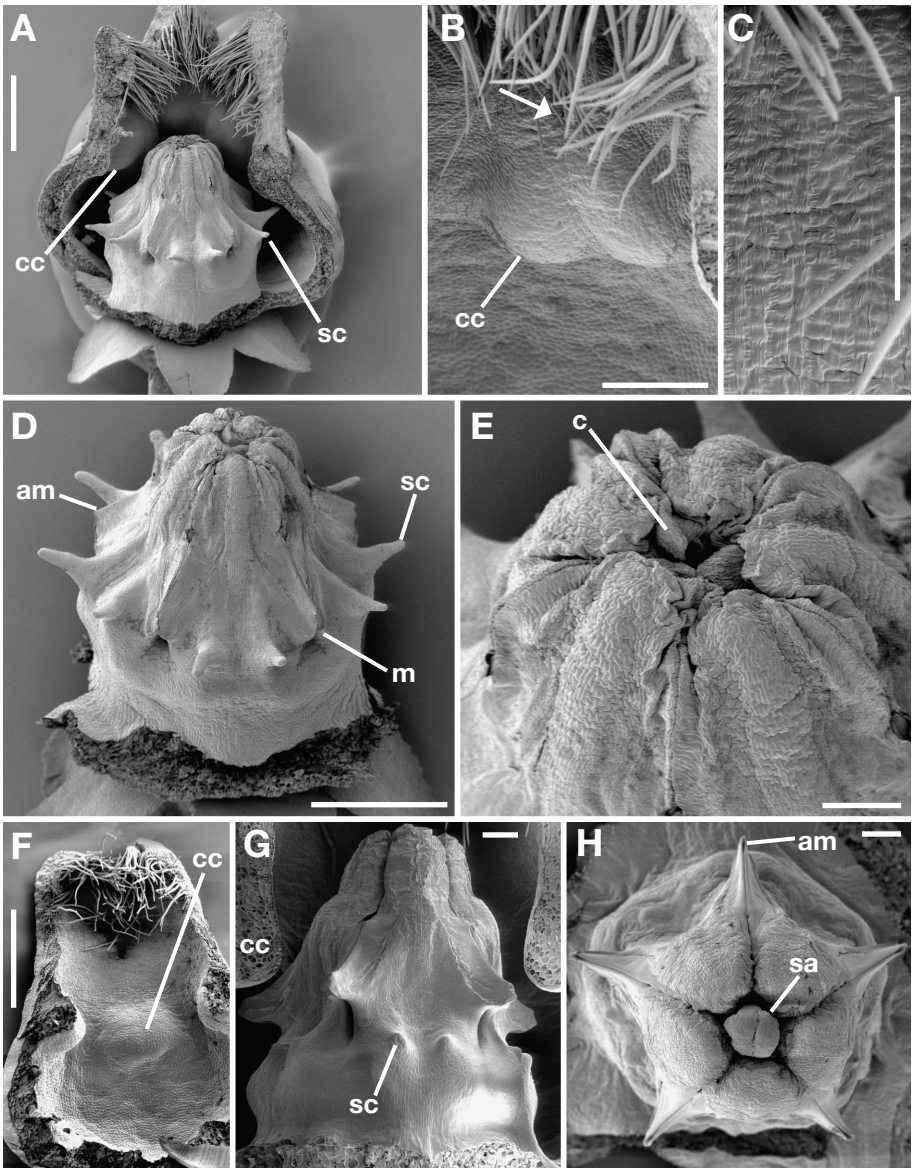

Fig. 3. A–E. *Dischidia cornuta* Livsh. A. Flower with half of corolla removed; B. corolline corona lobe; C. flat epidermal cells on adaxial surface of corolla lobes; D. gynostegium; E. apex of gynostegium. — F–H. *Dischidia imbricata* (Blume) Steud. F. Adaxial side of corolla with corolline corona lobe; G. gynostegium; H. apex of gynostegium (A–E: *Livshultz 02-50*; F–H: *Livshultz 99-7*). arrow = sinus between corolla lobes, am = anther margins, c = connective appendage, cc = corolline corona lobe, m = mouth at base of anther margin, sa = style-head apex, sc = staminal corona lobe. — Scale bars: A, D, F = 500 μm; B = 200 μm; C, E, G, H = 100 μm.

the gynostegium visible when flower viewed from above (not apparent in herbarium specimens). *Adaxial epidermal cells* except hair cells with flat anticlinal walls. *Corolline corona* consisting of 5 low, cordate lobes, 0.3 by 0.4 mm inserted in the corolla lobe sinuses (very obscure in herbarium specimens). *Gynostegium* 1–1.2 by 0.9 mm, conic in outline, stipitate. *Stipe* 0.3 mm tall, glabrous, pale yellow. *Anthers* triangular 0.7–0.8 by 0.5 mm, connectives reddish with triangular, white, hyaline appendages, c. 150 by 150 μm, covering the style-head apex, thecae white, anther margins with a very narrow mouth at the base. *Staminal corona* lobes each of 2 straight arms, c. 0.2 mm long, projecting perpendicular to vertical axis of the gynostegium, pale yellow. *Sclerenchyma* restricted to the anther margins, absent from staminal corona lobes. *Pollinarium* with pollinia acropetal to the corpuscle in situ. *Corpuscle* elliptic 190–200 by 60 μm, apex obtuse, rounded to truncate. *Caudicles* 240–250 by 130–140 μm at the widest dimension (at level of pollinium attachment), triangular, flattened, with a prominently thickened region along their inner edges and a small wing extending from the outer edges. *Pollinium* subterete, obovoid, 330–340 by 160–190 μm wide. *Carpels* 1.2 by 0.6 mm, obclavate, half terete, glabrous, green. *Style-head* radially five angled, obnapiform, 0.7 by 0.6 mm (including apex), green; apex 0.3 by 0.15 mm diam. at base, capitate, yellow, completely hidden by the anther connectives. *Fruit* 1 or follicles developing from each flower, pedicels 2.5–4 by c. 1 mm, follicles 3.7–4.9 by 0.65–0.8 cm diam., anguste ovate, apex obtuse, base rounded, half-terete to cordate in cross section, glabrous, glaucous, green with splotches of purple, turning tan when ripe, reflexed, forming an 90° or less angle with the pedicel. *Seeds* attached to a white, papery placenta, 2–3 by 0.7–1 mm diam., compressed-ovoid, obscurely winged on the margin, tan, testa smooth to sparsely papillate, glabrous; coma white.

Distribution — Known from southern Laos.

Habitat — Collected at 400–1000 m elevation.

Etymology — The specific epithet refers to the horn-like appearance of the staminal corona lobes.

Comments — *Dischidia cornuta* is obviously closely related to the widespread *D. imbricata* (Blume) Steud. (illustrated in Rintz, 1980), the only other shell-leaved species that occurs in Indochina. Both species lack calycine colleters, and have corollas of similar dimensions and colour with retrorse hairs on the lobe tips and flat adaxial epidermal cells. *Dischidia cornuta* and *D. imbricata* look identical without careful examination of the flowers (Table 2). The prominent staminal corona of *D. cornuta* (Fig. 3A, D) easily distinguishes it from *D. imbricata* which has a highly reduced staminal corona (Fig. 3G) that is often not evident in dried specimens. The corolline corona lobes of *D. cornuta* (Fig. 3B) are much less prominent than those of *D. imbricata* (Fig. 3F) and differ in shape (cordate vs ovoid). On herbarium sheets, *D. cornuta* appears to lack a corolline corona while that of *D. imbricata* is obvious. The shape of the anther margins is a somewhat subtle character but usually well preserved in herbarium specimens if the flowers are not too distorted by flattening. The anther margins of *D. imbricata* (Fig. 3G) project out prominently at their bases from the gynostegium, while those of *D. cornuta* (Fig. 3A, D) do not. Additional characters are visible in living or alcohol preserved flowers but obscured in herbarium specimens. The corolla lobes of *D. cornuta* are widely divergent and the gynostegium is visible when the flower is viewed from above (Fig. 2E); in *D. imbricata* the corolla lobes are slightly reflexed

Table 2. Comparison of morphological characters of *Dischidia cornuta* and *Dischidia imbricata*.

	D. cornuta	*D. imbricata*
corolla throat at anthesis	wide open, gynostegium visible from above	almost closed, gynostegium hidden by hairs
corolline corona lobes	cordate, not prominent	ovoidal, very prominent
staminal corona lobes	prominent, with long arms	obscure, with minute arms
base of anther margins	in close proximity to gynostegium	projecting out from gynostegium
style-head apex	covered by anther connective appendages	exposed, anther connective appendages tucked around it

but held close together at anthesis and the gynostegium is completely hidden from view by the retrorse hairs. The anther connective appendages of *D. cornuta* cover the style-head apex (Fig. 2E, 3E) while those of *D. imbricata* do not (Fig. 3H). Unlike *D. dohtii*, this character is often not apparent in herbarium specimens because the anthers of *D. imbricata* equal the style-head in height. Given that *D. imbricata* occurs in Thailand and Vietnam, sterile specimens from Indochina cannot be identified until the range and habitat of *D. cornuta* are better known.

Additional specimens:
Poilane 12136 (P), Laos, Chipon River, 400 m, 22 July 1925. *Livshultz 03-11* (BH), cultivated, field data: Laos, Champasak Province, Ban Thongset, Nong Khoum Khiaou, 15.20 N, 106.32 E, 1000 m, 5 Mar. 2003. *Livshultz 03-40* (BH), cultivated, field data: Laos, Champasak Province, Ban Thongset, Nong Khoum Khiaou, 15.20 N, 106.32 E, 1000 m, 7 Sept. 2003.

Dischidia dohtii Tran & Livsh., *spec. nov.* — Fig. 4, 5

Dischidia parvifoliae Ridl. affinis, sed foliis cordatis vel orbicularibus, indumento tenuiter lanato, et absentia appedicum staminalium basalium differens. — Typus: *Averyanov et al. 5197* (holo HN; iso A, MO), Vietnam, Kon Tum Province, Kon Plong District, Hieu Municipality, Mang La forest enterprise; primary evergreen broad-leaved wet forest with *Dacrycarpus imbricatus* on steep mountain slopes on sandstone and gneiss. Creeping epiphyte on high trees, Not common. 14.65 N, 108.42 E, 1100–1200 m, 14 April 2000.

Plants succulent, herbaceous, epiphytes, non-twining root-climbers forming mats on tree branches. *Roots* on mature plants adventitious, first roots always paired below each node, each root emerging opposite a leaf, within 2 elongated internodes on a actively growing shoot, additional roots produced along internodes. *Latex* white. *Indumentum* on all parts of plant except 3 inner floral whorls and roots sparsely lanate with simple, multiseriate (up to 8-celled), white hairs, 400–900 μm long, pubescence sparser on older parts, inflorescence bracts, pedicels, and calyces. *Wax chimneys* on stems and leaves absent. *Stems* terete, up to 1 mm diam.; internodes 0.8–1.3 cm long. *Stipular colleters* paired, triangular or ovate, to 0.3 mm long, inserted on either side of the petiole. *Leaves* always opposite, decussate early in development, becoming distichous, reddish when young becoming green at maturity except for small purple areas around colleters; petiole 1–1.5 by 0.4–0.5 mm, inserted on the leaf margin or slightly abaxially; mature lamina 0.5–1.3 by 0.5–1.5 cm, very succulent, biconvex, maximum thickness 0.6 cm (wrinkled in herbarium specimens), orbicular to compressed ovate, base rounded, truncate, to slightly cordate, bearing one triangular colleter, c. 0.1 mm long, on the

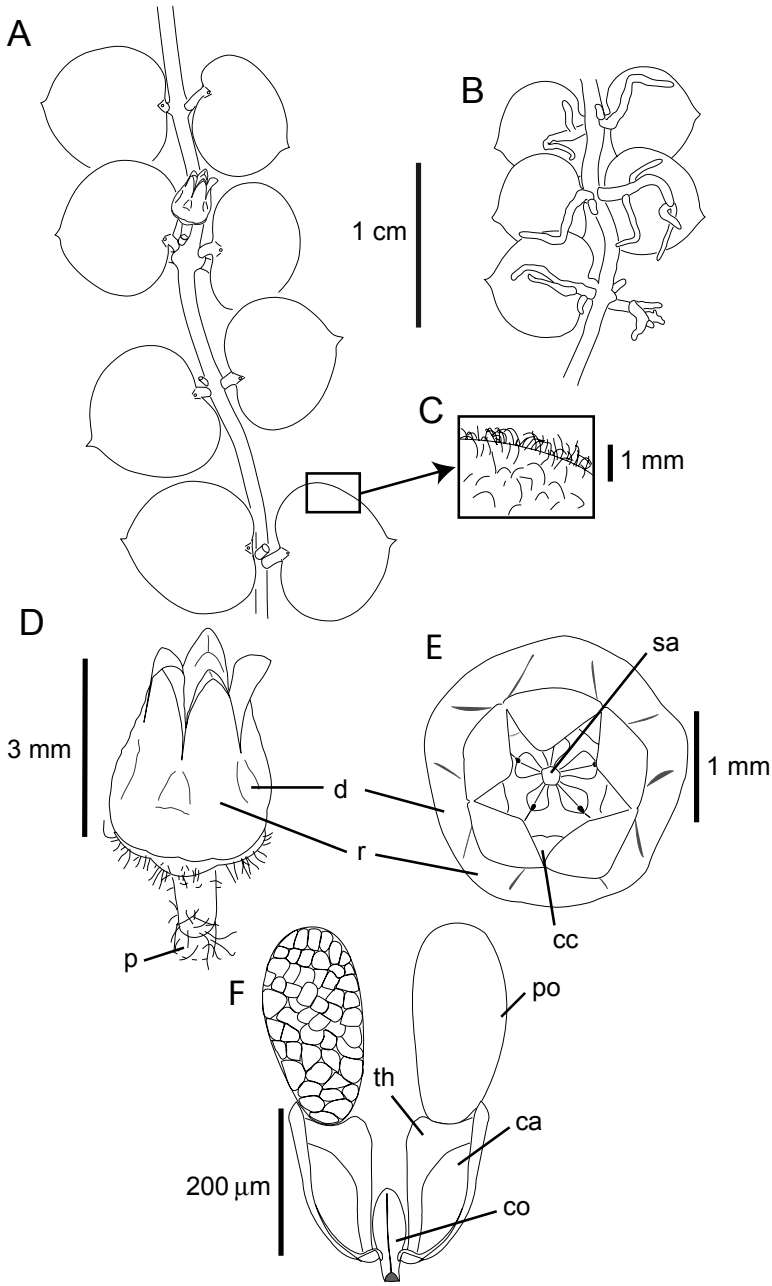

Fig. 4. *Dischidia dohtii* Tran & Livsh. A. Flowering shoot, upper side; B. shoot, underside with roots; C. lanate pubescence; D. inflorescence with single flower; E. flower viewed from above; F. pollinarium (A–E: *Livshultz 02-53*; F: *Averyanov et al. 5197*). ca = caudicle, cc = top of corolline corona lobe, co = corpuscle, d = depression on outer surface of corolla tube, p = peduncle, po = pollinium, r = rib along corolla tube below corolla lobe, sa = style-head apex, th = thickened part of caudicle. Drawn by D. Schott and T. Livshultz.

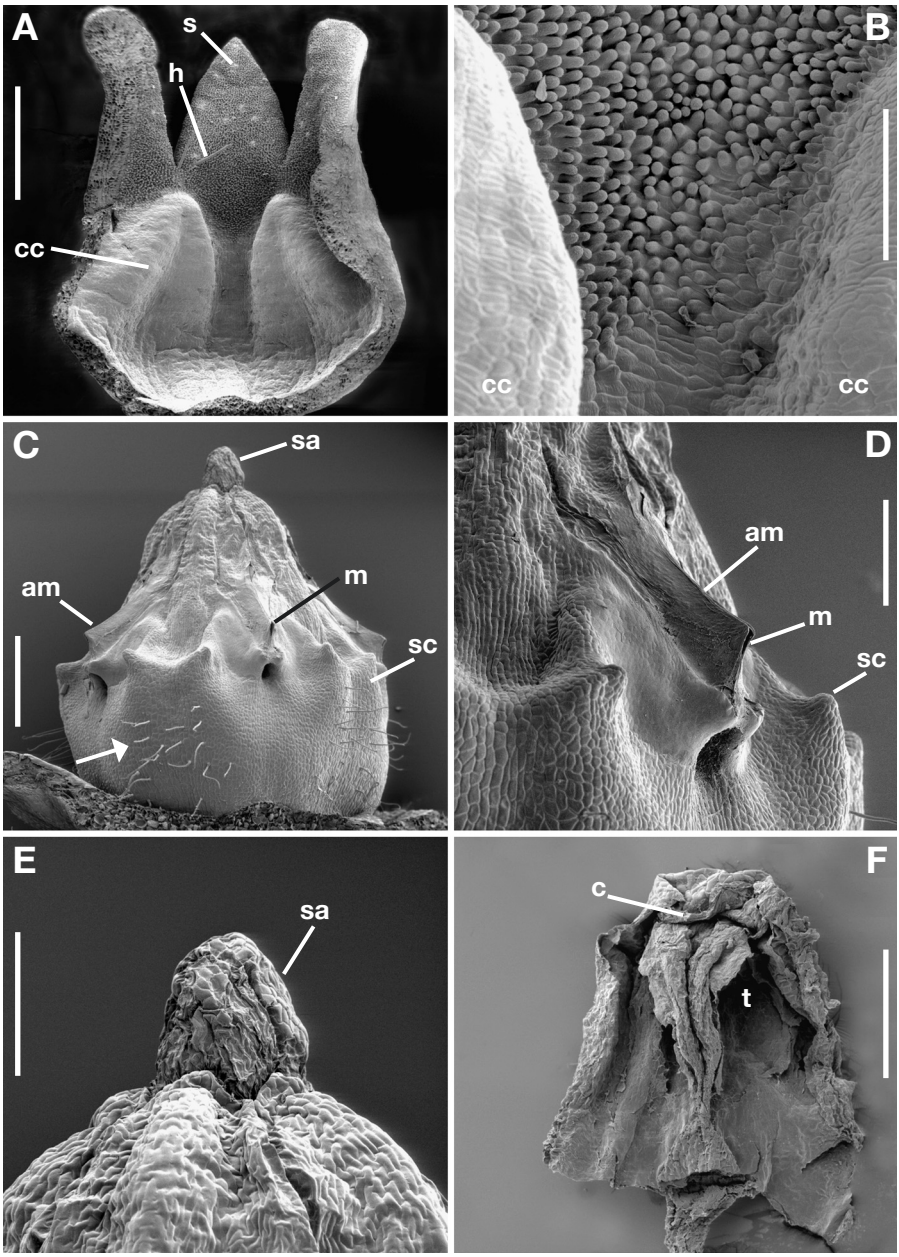

Fig. 5. *Dischidia dohtii* Tran & Livsh. A. Adaxial corolla surface; B. adaxial corolla surface close-up, papillate cells distally, flat cells proximally and on the corolline corona lobes; C. gynostegium; D. close up of anther margins and corona; E. close up of exposed style-head apex; F. anther viewed from adaxial side with folded over connective appendage (all: *Livshultz 02-53*). arrow = hairs on base of gynostegium, a = anther, am = anther margins, c = connective appendage, cc = corolline corona lobe, h = hair, m = mouth at base of anther margins, s = stomate, sa = style-head apex, sc = staminal corona lobe, t = thecum. — Scale bars: A, C = 250 μm; B, D–F= 100 μm.

adaxial side at the base of the midrib, apex apiculate (acute), secondary venation not visible. *Inflorescence* extra-axillary, peduncles < 1–2 by 1 mm, sparsely lanate, 1- or 2-flowered. *Flowers* each subtended by two bracts, bracts c. 0.5 by 0.5 mm, ovate to triangular, sparsely lanate, membranous (chartaceous in dried specimens). *Pedicels* 1.5 by 0.8 mm, glabrous to pubescent. *Calyx* lobes quincuncial in bud, 0.5 by 0.5 mm, ovate, apex obtuse, green with hyaline margins, sparsely lanate, bearing a colleter inside each lobe sinus, colleters ovate (cylindroid), 120–150(–450) by 90–110(–150) μm. *Corolla* succulent, urceolate, 3 by 2–2.5 mm at widest diameter, widest 0.5 mm from the base, 5-ribbed, with triangular depressions opposite the sinuses (not evident in dried specimens), tube pale yellowish to off-white, lobes reddish in young buds fading to very pale peach-pink or off-white on the abaxial surface at anthesis, adaxial corolla surface pure white; corolla lobes valvate in bud, reflexed at anthesis, 0.7 by 0.4–0.5 mm, triangular, succulent, with slightly cucullate tips, with small, stomate-bearing papillae on the abaxial surface, adaxial surface also with scattered stomates, glabrous or with sparse scattered hairs on the lower part of the corolla lobes and at the throat; throat c. 1 mm diam., the gynostegium visible when flower is viewed from above. *Adaxial epidermal cells* uniformly papillate (except for stomatal complexes) on the corolla lobes, papillate cells extending on to the upper portion of the corolla tube opposite the corolla lobe, cells of the corolline corona lobes and lower portion of the corolla tube with flat anticlinal walls. *Corolline corona* consisting of 5 prominent chevron-shaped wedges, each 0.7 by 0.5 mm, inserted adaxially in the sinuses of the corolla lobes. *Gynostegium* 1.5 by 1.2 mm, conic in outline, stipitate. *Stipe* 0.6 mm long (measurement from insertion on corolla tube to opening below anther margins), white, bearing long hairs on the zone below each staminal corona lobe. *Anthers* triangular, 0.9 by 0.6 mm, yellow with a longitudinal red stripe on each thecum, apical connective appendages 100 by 250 μm, ovate, hyaline, held folded over the thecae, tucked around the style-head apex, not covering its tip, adjacent anther margins forming a very narrow mouth at the base. *Staminal corona* of five, unstalked lobes inserted at the bases of the anthers, each lobe with two minute arms, and a retuse apex, white, without sclerenchyma (staminal corona often appearing as absent in pressed, dried specimens). *Sclerenchyma* restricted to the anther margins. *Pollinarium* with pollinia acropetal to the corpuscle in situ. *Corpuscle* elliptic 130–150 by 40–50 μm wide, apex obtuse, rounded to truncate. *Caudicles* 240 by 70–90 μm at the widest dimension (at level of pollinium attachment), triangular, flattened, with a prominently thickened region along their inner edges and a small wing extending from the outer edges. *Pollinium* dorsiventrally flattened, elliptic, apex obtuse, 250–290 by 90–100 μm. *Carpels* 0.9 by 0.5 mm, obclavate, half terete, glabrous, green. *Style-head* radially five angled, obnapiform, 0.7 by 0.6 mm (including apex), yellow, apex cylindrical, 0.3 by 0.15 mm, its distal half purple, projecting above the anthers. *Fruit* unknown.

Distribution — Collected from southern Laos and central Vietnam.

Habitat — 1000–1200 m elevation.

Etymology — *Dischidia dohtii* (dōtēī) is named after Doth Laounmuang, director of Project Green Life, an education and conservation initiative working to protect the forest at Nong Khoum Khiaou in Champasak Province, Laos. The transliteration of Mr. Laounmuang's name has been modified to facilitate correct pronunciation of the species epithet by English speakers.

Comments — Of other species in Vietnam and Laos, *D. dohtii* is most likely to be confused with *D. nummularia* R.Br. (illustrated in Rintz, 1980). The two species have the same creeping, non-twining growth habit, similar succulent, apiculate, orbicular leaves, short, few-flowered peduncles, and small whitish flowers. The two species can easily be distinguished by characteristics of the vegetative epidermis which is sparse lanate, without wax chimneys in *D. dohtii* and glabrous, with wax chimneys in *D. nummularia*. A few herbarium specimens of *D. nummularia* lack wax chimneys, probably due to artefacts of preservation such as flaking off of the epicuticular wax or coating of the specimen with glue, or possibly collection of very young or mesic branches. Such specimens can still be distinguished from *D. dohtii* by their lack of pubescence and by floral characters. The most obvious floral character is the reduced (often appearing as absent in herbarium specimens) staminal corona of *D. dohtii* vs the prominent stalked, anchor-shaped corona lobes of *D. nummularia* (illustrated in Rintz, 1980). The exposed style-head apex of *D. dohtii* and the covered style-head apex of *D. nummularia* are also reliably preserved on herbarium specimens. Habitat is also a good clue, since *D. nummularia* is consistently a lowland species while *D. dohtii* appears to be restricted to highland areas. The two species are compared in Table 3. The very long, cylindroid calycine colleters found in some flowers of *D. dohtii* are very distinctive but they cannot be considered a species character since they are only rarely present. The absence of condensed, bracteate inflorescence axes on our specimens also should not be considered as a species character. These axes develop with successive cycles of flowering, and given that *D. dohtii* only produces 1 or 2 flowers at a time, may take a long time to develop in this species.

In spite of the superficial similarity of *D. dohtii* to *D. nummularia*, *D. dohtii* is probably more closely related to *D. parvifolia* Ridl., a highland endemic from Peninsular

Table 3. Comparison of morphological characters of *Dischidia dohtii* with *Dischidia parvifolia, Dischidia nummularia*, and *Dischidia khasiana*.

	D. dohtii	*D. parvifolia*	*D. nummularia*	*D. khasiana*
wax chimneys on leaves and stems	absent	absent	present (absent)	absent
indumentum	sparse lanate	tomentose-papillate, glabrescent	glabrous	tomentose-papillate, glabrescent
pedicel length (mm)	1.5	2.5–5	1–2	3 (in fruit)
hairs inside corolla tube	absent or sparse on bases of corolla lobes and at throat	absent	more or less dense on bases of corolla lobes	unknown
adaxial epidermal cells of corolla lobes and distal corolla tube	papillate	papillate	flat	unknown
hairs on the gynostegial stipe	present	present	absent	unknown
staminal corona segment	small lobe with minute arms, may appear as absent	small lobe without arms, may appear as absent	prominent, stalked, anchor-shaped lobe with well-developed recurved arms, always evident	unknown

Malaysia (illustrated in Rintz, 1980). Both species lack wax chimneys on their vegetative organs, have papillate epidermal cells on the adaxial surface of the corolla lobes, pubescent gynostegial stipes, reduced staminal coronas, and protruding style-head apices that are not hidden by the anther connective appendages (Table 3). *Dischidia dohtii* can easily be distinguished from *D. parvifolia* by leaf shape and indumentum (orbicular to cordate and lanate vs ovate and tomentose to glabrescent) and pedicel length (1.5 mm vs 2.5–5 mm) (Table 3). The anthers of *D. parvifolia* have prominent basal appendages, giving them a distinctly sagittate appearance; no such appendages are present in *D. dohtii*.

Additional specimens:
Livshultz 02-53 (BH, National University of Lao), cultivated, field data: Laos, Champasak Province, Ban Thongset, Nong Khoum Khiaou, 15.20 N, 106.32 E, 1000 m, 23 Sept. 2002.

Dischidia khasiana Hook.f. — Fig. 6A, B

Dischidia khasiana Hook.f. (1885) 50; A.P. Jagtap & N.P. Singh (1999) 74. — Type: *Hooker f. & T. Thomson 9* (lecto K, designated here, isolecto A, G, L), India, Megalaya Province, Khasia Mountains at Churra and Nunklow, alt. 3–4000 ft.

Comments — The enigmatic *D. khasiana* Hook.f., known from a single fruiting collection, might also be related to *D. dohtii*. Both species have small, orbicular, apiculate leaves, no wax chimneys, and unbranched inflorescences with short peduncles. Both occur around 1000 m elevation. The two species can be differentiated by their

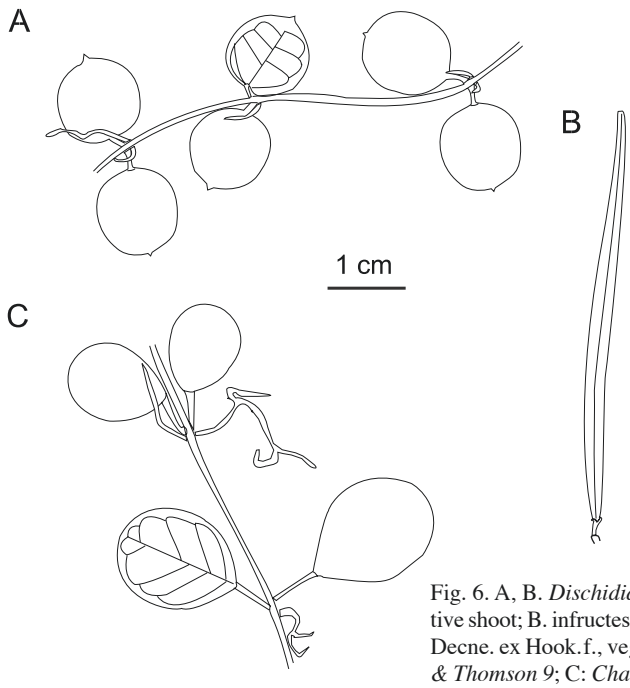

Fig. 6. A, B. *Dischidia khasiana* Hook.f. A. Vegetative shoot; B. infructescence. — C. *Hoya nummularia* Decne. ex Hook.f., vegetative shoot (A, B: *Hooker f. & Thomson 9*; C: *Chatterjee & Saha 13598*). Drawn by T. Livshultz.

indumentum: sparse lanate, hairs 400–900 μm long, in *D. dohtii*, tomentose to glabrescent, hairs 100–200 μm long, in *D. khasiana*. The type of *D. khasiana* is a mixed collection with *Hoya nummularia* Decne. ex Hook.f. One of the sheets at K is entirely material of *Dischidia khasiana* while the other is predominantly *H. nummularia*. The sheets at A, G, and L are predominantly or entirely *D. khasiana*, while sheets at M and C are predominantly or entirely *H. nummularia*. Flowers of *H. nummularia* are present on the sheet from M. *Hoya nummularia* (Fig. 5C) also has small orbicular leaves, but its leaf apices are obtuse, not apiculate, and its petioles (3–7 mm), peduncles (50 mm long) and pedicels (20–25 mm) are much longer than those of *D. khasiana* (petioles 1–2(–3) mm, peduncles 1 mm, pedicels 3 mm).

Dischidia khasiana Hook.f. is here lectotypified by the sheet deposited at K, annotated by the senior author, that does not contain any material of *H. nummularia*.

Dischidia rimicola Kerr — Fig. 7, 8

Dischidia rimicola Kerr (1939) 463; Craib & Kerr (1951) 47. — Type: *Put 2984* (K), Thailand, Krat, Kao Kuap, 24 May 1930.

Plants succulent, herbaceous, epiphytic vines, with a tendency to grow from a single root stock rather than to cling by adventitious roots, pendulous and twining. *Roots* on mature plants adventitious, first roots paired or solitary, each root initiated in a leaf axile, 5–10 elongate internodes below the apex of an actively growing stem, additional adventitious roots frequently produced near each node and along the internodes. *Latex* white. *Indumentum* tomentose, hairs curling, simple, uniseriate, 0.1–0.2 mm long on all parts except the inner three floral whorls and roots, hairs sparser (rarely absent) on older stems, limited to near the margins and petioles of mature leaves. *Wax chimneys* absent. *Stems* terete; 1–2 mm diam.; internodes 1.5–9.5 cm long. *Stipular colleters* paired, triangular or ovate, to 0.1 mm long, inserted on either side of each petiole. *Leaves* always opposite, decussate early in development, becoming distichous; petiole 1–3.5 by 0.8–1 mm, inserted on blade margin; blade 1.7–3 by 0.8–1.3 cm, ovate or elliptic, apex acute to acuminate, base cuneate to rounded, with slightly involute margins in younger leaves, plano (adaxial-)convex (abaxial) in older leaves, 1–3 mm thick, bearing a single ovate colleter c. 0.1 mm long at the base of the adaxial surface; venation obscure in living plants, prominent in herbarium specimens, brochidodromous with 2–5 secondaries on each side of the midrib. *Inflorescence* extra-axillary, umbelliform, persistent through many flowering cycles, sessile, a single, condensed axis bearing 3–7 flowers and buds at various stages of maturity, 1 or 2 flowers simultaneously at anthesis; lower portions of axis bearing scars and bracts from fallen flowers. *Flowers* subtended by two membranous triangular to lunate, glabrous to sparse pubescent bracts, c. 0.5 by 0.5 mm, the bracts becoming chartaceous, persistent after flowers fall, but wearing off from the oldest parts of the rachis. *Pedicels* 1.5–2 by 0.5 mm, pale green, glabrous or sparse pubescent. *Calyx* lobes quincuncial in bud, 0.6–0.7 by 0.5–0.6 mm, triangular to ovate, apex obtuse to acute, sparsely pubescent abaxially, pale green sometimes with purple pigment on the tips, with hyaline margins, margins ciliate or not, with a single minute colleter inside each sinus. *Corolla* succulent, full of nectar, urceolate, 3.5–4 by 2.5 mm at widest diameter, widest c. 0.5 mm from the base, 5-lobed at base, lobes opposite the sepals, abaxially with stomate bearing papillae, corolla cream-white with

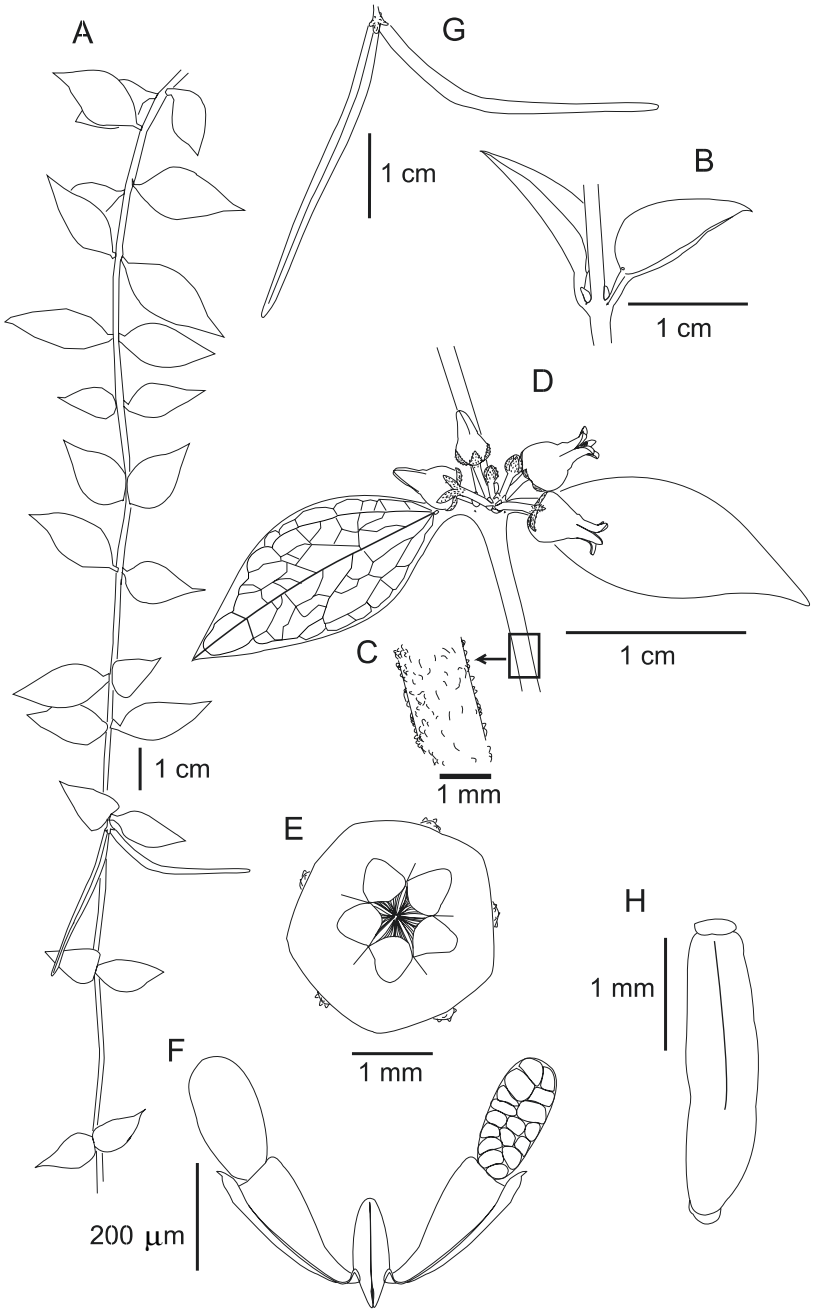

Fig. 7. *Dischidia rimicola* Kerr. A. Fruiting shoot; B. node with first adventitious roots initiated in the leaf axils; C. tomentose pubescence on stem; D. node with inflorescence; E. flower at anthesis viewed from above; F. pollinarium, slight thickening of caudicle not depicted because it is not visible with light microscopy; G. fruit; H. seed without coma (A, G: drawn from photo, population vouchered by *Livshultz 01-24*; B–F: *Livshultz 01-24*; H: *Poilane 28421*). Drawn by T. Livshultz.

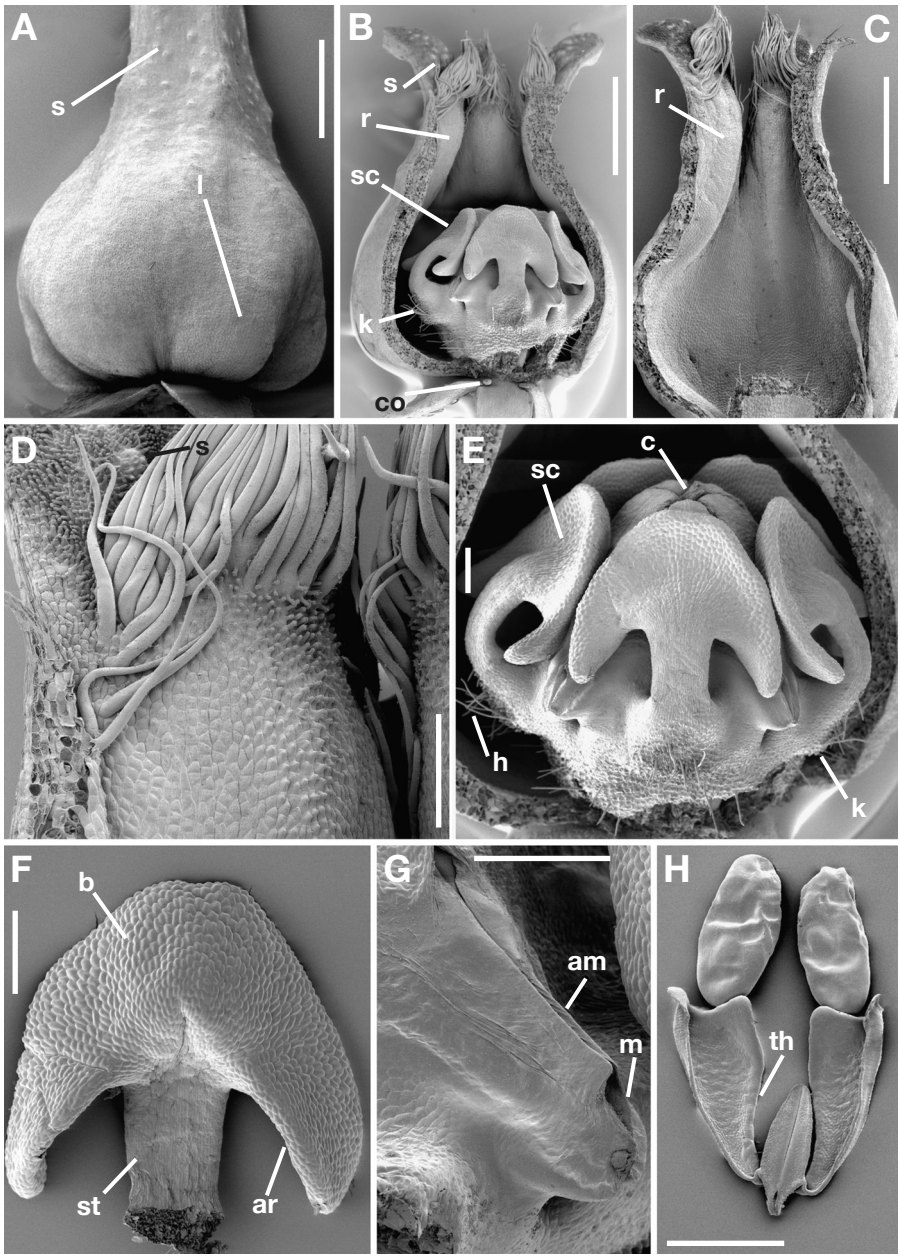

Fig. 8. *Dischidia rimicola* Kerr. A. Base of corolla tube of bud near anthesis; B. flower with 2 petals removed; C. adaxial side of corolla; D. adaxial surface of corolla lobe; E. gynostegium; F. adaxial surface of staminal corona lobe; G. anther margins; H. pollinarium (all: *Livshultz 01-24)*. am = anther margins, ar = arm, b = blade, c = connective appendage, co = colleter, h = hair, k = knob at base of staminal corona lobe, l = basal lobe of corolla tube, m = mouth at base of anther margins, r = rib, s = stomate, sc = staminal corona lobe, st = stalk, th = thickening of inner margin of caudicle. — Scale bars: A = 200 μm; B, C = 500 μm; D–H = 100 μm.

or without purple pigment on adaxial or abaxial surface of the corolla lobe tips. *Corolla lobes* valvate in bud, 1.5–1.8 by 0.7–1 mm, triangular, each with a low rounded rib adaxially that extends into upper part of the tube, tips only slightly thickened adaxially, at anthesis remaining connivent along their margins for c. 50% of their length, diverging distally, each bearing a wedge of long, straight, antrorse hairs near its centre, wedges forming a cone of hairs closing the corolla throat and hiding the gynostegium. *Adaxial epidermal cells* (except stomatal complexes) papillate above the hairs, flat below them except for a few papillate cells along the midline of the rib. *Corolline corona* absent. *Gynostegium* 1.2–1.4 m by c. 1.2 mm, conic in outline, stipitate. *Stipe* c. 0.4 mm tall (measurement from insertion on corolla tube to opening below anther margins), pubescent with tufts of hairs below each staminal corona lobe. *Anthers* triangular 0.8–1 by 0.8–1 mm; connectives purple with triangular, white, hyaline appendages covering the style-head apex; thecae white; anther margins forming an elliptic mouth at their base. *Staminal corona* of five white, membranous lobes inserted at the bases of the anthers, each lobe with a small, pubescent knob at its base, stalked with sagittate apex, stalk 200 by 100 μm, apex 250 by 450 μm, concave abaxially, convex adaxially, with obtuse, entire apical margin, arms falcate, 150 μm long. *Sclerenchyma* restricted to the anther margins, and along the margins of the staminal corona lobe apex. *Pollinarium* with pollinia acropetal to the corpuscle in situ. *Corpuscle* elliptic 200–210 by 70 μm, apex obtuse, rounded to truncate. *Caudicles* 310–330 by100–120 μm at the widest dimension (at level of pollinium attachment), triangular, flattened, with very slightly thickened regions along their inner edges (not evident with light microscopy) and small wings extending from the outer edges. *Pollinium* elliptic, compressed, 240–260 by 110–130 μm. *Carpels* 0.7 by 0.4 mm, obclavate, half-terete. *Style-head* radially 5-angled, turbinate, 0.4–0.5 by 0.6–0.7 mm (including apex), pale yellow, apex a small papilla, c. 0.1 mm tall, pale yellow. *Fruit* 1 or 2 follicles developing from each flower, pedicels 2–2.5 by c. 1 mm, follicles 4–5 by 0.2 cm diam., linear, glabrous, green turning tan when ripe, forming a 120–180° angle with the pedicel. *Seeds* attached to a white, papery placenta, 2.5–2.7 by 0.5–0.6 mm diam., ellipsoid, terete to subterete, wing restricted to chalazal end, testa papillate, glabrous, tan; coma white.

Distribution — Known from Thailand, Laos, and Vietnam, may also occur in Cambodia.

Habitat — All collections of *D. rimicola* are from elevations at or above 1000 m.

Comments — *Dischidia rimicola* belongs to a potentially monophyletic group of species distinguished by long, narrow, basally connivent, distally reflexed corolla lobes with antrorse hairs on the middle of the lobe, no corolline corona, and stalked staminal corona lobes with sagittate apices. This group also includes *D. formosana* Maxim. from Taiwan (illustrated in Lu & Kao, 1978), *D. scortechinii* King & Gamble from Malaysia (illustrated in Rintz, 1980), *D. singularis* Craib and *D. tricholoba* Kerr from Indochina (Table 4). *Dischidia singularis* has cross-shaped leaves with two lateral lobes and is impossible to mistake for any other species. *Dischidia tricholoba* has ovate to elliptic leaves and is more likely to be mistaken for *D. rimicola*, especially Vietnamese specimens which have markedly smaller leaves than Thai plants, 1.2–2.3 vs 3.5–7 cm long. *Dischidia tricholoba* can be reliably distinguished from *D. rimicola* by its usually glabrous stems and calyces, larger flowers (5 vs 3.5–4 mm), absence of ribs on the adaxial sides of the corolla lobes, and absence of hairs on the gynostegial stipe (Table 4).

Table 4. Comparison of morphological characters of *Dischidia rimicola, Dischidia singularis,* and *Dischidia tricholoba*.

	D. rimicola	*D. singularis*	*D. tricholoba*
mature leaf lamina length by width (cm) and shape	1.7–3 by 0.8–1.3 elliptic, ovate, apex acute-acuminate, base cuneate to rounded	3.5–5.5 by 0.7–0.8 cross-shaped with 2 lateral lobes, apex acute-apiculate, base cuneate to rounded	1.2–7 by 0.5–3 ovate, elliptic, apex acute, base rounded to cuneate
stem indumentum	tomentose, glabrescent	glabrous (sparse pubescent)	glabrous (sparse pubescent)
calyx indumentum	tomentose	glabrous	glabrous (very sparse pubescent)
corolla length by diameter (mm) (hydrated)	3.5–4 by 2.5	3–3.5 by 2	5 by 2–2.5
ribs on adaxial side of corolla lobes	present	absent	absent
hairs on gynostegial stipe	prominent tuft below staminal corona lobe	absent (minute pubescent)	absent
staminal corona lobe	stalked, apex sagittate with prominent arms	stalked, apex semi-lunate with very reduced arms	stalked, apex sagittate with prominent arms

It is possible that *D. tricholoba* is not a distinct species but only the juvenile growth form of *D. singularis*. *Dischidia singularis* was described as having dimorphic juvenile and adult foliage (Craib & Kerr, 1951), and specimens identified as the juvenile form of *D. singularis* match the type of *D. tricholoba* (*Kerr 7775,* K). Plants with both morphologies are sympatric in Thailand, but we have not seen any specimens with both types of foliage on the same plant. *Dischidia tricholoba* and *D. singularis* differ not only in leaf shape but also in flower size and staminal corona lobe shape (Table 4). We will recognize *D. singularis* and *D. tricholoba* as distinct species until we see evidence to the contrary.

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IDENTIFICATION LIST

Collections are identified according to the species list below. Unnumbered collections are not included. Collections from institutions are listed under the abbreviation of the institution with the collectors' names in parentheses after the specimen numbers. Components of mixed collections are identified by the abbreviation 'p.p.'.

1. *Dischidia acuminata* Costantin
2. *Dischidia acutifolia* Maingay ex. Hook.f.
3. *Dischidia bengalensis* Colebr.
4. *Dischidia cornuta* Livsh.
5. *Dischidia dohtii* Tran & Livsh.
6. *Dischidia formosana* Maxim.
7. *Dischidia griffithii* Griff. ex Hook.f.
8. *Dischidia hirsuta* (Blume) Decne.
9. *Dischidia imbricata* (Blume) Steud.
10. *Dischidia khasiana* Hook.f.
11. *Dischidia major* (Vahl) Merr.
12. *Dischidia nummularia* R.Br.
13. *Dischidia oiantha* Schltr.
14. *Dischidia parvifolia* Ridl.
15. *Dischidia rimicola* Kerr
16. *Dischidia scortechinii* King & Gamble
17. *Dischidia singularis* Craib
18. *Dischidia tonkinensis* Costantin
19. *Dischidia tricholoba* Kerr
20. *Hoya nummularia* Decne. ex Hook.f.

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